A NEW TOOTH-PLATED DIPNOAN FROM THE UPPER DEVONIAN GOGO FORMATION AND ITS RELATIONSHIPS

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The commonest dipnoan species from the Frasnian Gogo Formation are *Chirodipterus australis* Miles and *Griphognathus whitei* Miles. Less abundant species are *Holodipterus gogoensis* Miles and other holodipterids, *Pillararhynchus longi* Barwick & Campbell, and *Gogodipterus paddyensis* (Miles). One would have expected many more representatives of tooth-plated forms of the *Dipterus*-type in the Late Devonian Gogo faunas. Recently a small number of individuals belonging to the tooth-plated group have been discovered, two of them being adults and one juvenile. They have been prepared to show how tooth-plates of this kind grew, and the outstanding features they produce in adults. They have been assigned to *Adololopas moyasmithae* gen. et sp. nov. Histology of the tooth-plates has been investigated optically and by SEM. The cores of the teeth are composed of hypermineralised dentine with abundant dentine tubules; the pallial dentine is thick in the distal teeth where it is supported on a ring of pedestal dentine. The heels of the plates are composed of solid dentine of the kind that forms the core of the teeth. The basal pulp cavity is continuous beneath the tooth rows, but it is joined to the underlying bone at well defined patches. A Late Devonian (Frasnian) Canadian genus *Scaumenacia*, has been studied with a view to adding further information to a wider study of tooth-plate evolution. Consideration is given to the reasons why long-headedness has to be further analysed before it can be used for taxonomic purposes.

☐ *Devonian, Dipnoi, tooth-plates, Gogo Formation.*

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Acid-etched nodules from the Gogo Formation occasionally contain dental plates carrying real teeth. These teeth are not associated with intact skulls, as is usual for Gogo dipnoans; one well-preserved body indicated that a complete skull should have been present, had it been well-ossified. We have been reluctant to proceed with a description and taxonomic designation until more data on the skull roof became available. We have now etched most of the material available to us, and no well-ossified skull has appeared with teeth like those of the fragmentary material; consequently we are describing this material on the assumption that it will be some time before further specimens are discovered. The new information, though incomplete, is valuable for interpreting the Late Devonian history of the Dipnoi.

Three specimens are available — an adult and a juvenile held at the Geology Department, Australian National University (ANU) and an adult in the Western Australian Museum (WAM). The ANU adult was prepared from a nodule without first embedding it in plastic. As a result, all the parts are free and available for reassembly. The WAM specimen was split along the axis of the fish at the time of collection. Because of this, it was embedded in plastic prior to etching, so that it could be better held together during preparation. Subsequently, the anterior part of one side of the preparation was treated with chloroform to loosen the plastic, and several isolated bones and a pair of tooth plates were obtained. These have proved especially valuable in understanding the histology of the tooth-plates. In the following discussion we have been able to provide separate descriptions of the macromorphology, micromorphology and histology of the tooth-plates of our new species.

SYSTEMATIC PALAEONTOLOGY

Order SPEONESIDRIONINA Campbell & Barwick, 1990

REMARKS. We continue to reject cladistic analyses that use all the so-called synapomorphic characters as of equal value in establishing relationships. We contend that a complete analysis of a group of taxa is much more likely to be achieved by an examination of a number of related functional characteristics. Our 1990 analysis indicated that during the Early Devonian, dipnoans used three different methods of covering the palate and prearticular bones with dentine-bearing protuberances.

Denison (1974: 32) indicated that early dipnoan types had very different dental apparatuses, and that there was little indication "that 'plateless' genera were derived from nor closely related to those with dental plates". We considered that the three dental types referred to above, tooth-plated, dentine-plated and denticulate, are quite different in the organisation of other features in addition to the teeth, and once they were established they apparently did not alter from one type of organisation to another. This approach was attacked mainly because we did not regard the presence of denticles as always indicating a primitive condition, as though we had proposed the presence or absence of denticles in the mouth as the sole criterion of relationships. Although we used the dominance of denticles as a basis for naming one of the types, nowhere did we espouse the view that the presence of denticles is the sole defining feature of the group. To the contrary, we have pointed out that each type is organised so as to have a number of features correlated with the different types of food reduction (Campbell & Barwick, 1987, 1990; Barwick, Campbell & Mark-Kurik, 1997).

One of the three types outlined above had tooth-plates formed by teeth that were arranged in rows; new teeth having been formed at the distal end of each row. Members of this group we assigned to the Order Speonesydrionina. The teeth were described as having a cover of enamel (enameloid) over a thin layer of pallial dentine, which covered a thick and dense layer of heavily mineralised dentine. Dental plates of this type we have previously termed tooth-plated, as opposed to the dentine-plated types that had no true teeth at the plate margins (Smith & Campbell, 1987).

In a further criticism of our basic approach, Kemp (1992) has pointed out that some of the genera we assigned to non-denticulate groups, do in fact have teeth in the early growth stages, but have lost them in adulthood. She referred to the Late Devonian lungfish fossils from the Coffee Hill Member, Catombal, near Orange, NSW in which juveniles, up to 3mm x 4mm, some of which may have been *Chirodipterus*, may have had teeth in the early growth stages. In 1994 she considered that 'many lungfish of Devonian age, like *Chirodipterus*, previously regarded as having solid dental plates, are in fact built up from cusps that fuse at their bases to form tooth plates with radiating ridges. ... *Chirodipterus* is definitely one of the tooth plated lungfishes'. Nowhere has she shown that *Chirodipterus* occurs in the Catombal fauna, a difficult thing to do in the absence of skeletal features other than tooth-plates. Until her material is described, and evidence of the existence of *Chirodipterus* of the *C. australis* type in the Catombal faunas is provided, we do not see that our analysis is in any way effected.

FAMILY INCERTAE SEDIS

REMARKS. In 1990 we separated late Palaeozoic tooth-plated dipnoans from *Dipterus* because they had no separate K bone, no lateral line in bone J, no buccohypophysial canal, unossified otic part of the braincase, and a partly buried pectoral girdle. *Adololopas* has a separate K, a canal in J, and an unossified braincase, but it lacks a buccohypophysial canal opening, and its girdle is largely buried. Hence it does not fall easily into the *Dipterus* group or the alternative non-*Dipterus* group on the characters defined in 1990. This view is supported by the elongate size of the cheek in the new genus *Adololopas*, the peculiar position of the lateral lines on the posterior part of the head, and the advanced nature of the dental plates with large basal pulp cavities. In addition it has a lateral line emerging from bone I to run along the body, a feature not observed in any other tooth-plated form apart from *Gnathorhiza*. We do not have access to the external parts of the mandible and the anterior part of the mandible which would also enable us to clarify the phylogenetic relationships. All this illustrates the difficulty of defining larger taxonomic groups on a number of characters which evolve considerably during time. Whatever the outcome, we now accept that *Adololopas* cannot be placed definitely in the Dipteridae, but we will not make a new Family to include it, because many features of the genus cannot be determined on present material.

Adololopas has a more advanced tooth-plate structure than *Dipterus*. Although *Dipterus* has for many years been regarded a member of the tooth-plated group, and forms assigned to it are very widely known throughout the world, the dental characteristics of specimens from the type locality are not very well preserved. Smith (1984) described the teeth of *Dipterus valenciennesi* from Scottish specimens. No other Middle Devonian genus showing the details of the tooth-plates has been described, but Elga Mark-Kurik has given us some incomplete Middle Devonian specimens. These are being described elsewhere in a separate paper (Campbell & Barwick, in press). These specimens provide an example of the extent to which the plate structure had evolved during the Middle Devonian.

Adololopas gen. nov.

ETYMOLOGY. Greek *adolos*, true; Greek *lopas*, plate.

TYPE SPECIES. *A. moyasmithae* sp. nov. from the Frasnian (Upper Devonian) of the Gogo Formation, Canning Basin, Western Australia.

DIAGNOSIS. Endocranium poorly ossified. Dermal roofing bones not tightly sutured together, cosmine covered; bone B long and narrow, and with scalloped margins; bone I transmitting a lateral line canal from Y_1 to bone Z; no Y_2 preserved, but judging from the position of 8 and the shape of the opercular, it must have been present; bones 4, 5 and 8 unusually long for a tooth-plated form of this age; snout well-ossified. Adult pterygoidal tooth-plates thick, with an open median suture and with 6-7 rows of teeth; new conical teeth added at ends of rows, and mounted directly on bone; mandibular tooth plates showing teeth added sufficiently deeply to be out of occlusion but growing up into occlusion as they increase in size; adult tooth-plates with thin primitive dentine and serrated edges along the posterior margins; palatal tooth-plates concave, and mandibular plates convex. Juvenile tooth-plates with six or seven rows of sharp teeth; continuous rings of enamel- or enameloid-covered primitive dentine around the posterior, lateral and mesial edges. Parasphenoid with ploughshare shape, pointed posterior extremity and closed buccohypophysial canal lying in its anterior keel. Dentary narrow; angular bone with a deep notch posteriorly for articulation of the surangular. Body short and rapidly tapering; scales similar in form to those of *Chirodipterus australis,* but their size diminishes rapidly towards the tail and the dorsal margin.

REMARKS. This genus is noteworthy in having the lateral line canal running from bone I on the skull roof to the body. The only other genera in which this is known are *Gnathorhiza* and *Jarvikia* (Campbell & Barwick 1990, figs 4, 5). This interpretation of *Jarvikia* has been questioned by Schultze & Marshall (1993), who claimed that the connection of the main lateral line of the body with that of the skull roof through bone I is unique for *Gnathorhiza*. The specimen that shows the detail for *Jarvikia* is the paratype of *J. arctica* Lehman (1959, pl. 20B, fig. 22). One of us, KSWC, has examined Lehman's specimens, and considers that his photograph gives an incomplete impression of the lateral line canals. This inaccuracy is also shown in his figure 22. Herein we produce new photographs of the same specimen showing the canals effectively (Fig. 2A,B). The canal runs posteromesially from the bone we interpret as Y into bone I (Campbell & Barwick, 1990, fig. 5). There the canal splits to produce a branch across bone B, and a second one backwards lateral to the process on the posterior end of the bone I, where it joins the main body lateral line canal. There is no other posteriorly directed canal from Y. The situation described is certainly unusual for the dipnoans, but we reject the statement of Schultze & Marshall (1993, p. 216) that our view on this feature is a 'mistake in our morphological analysis'. The new photographs show that the canal is clearly present as we have indicated. The palate of *Jarvikia* is not well known; Lehman (1959) recorded that the genus did not have tooth plates, but probably had a denticulated palate. One of us, KSWC, has been able to confirm that judgement by observation of the original specimens. The arrangement of the overlap between the pterygoids and the peculiar relationships of the parasphenoid, demonstrate that *Jarvikia* and *Adololopas* are distantly related. We see no reason to group these genera together on the basis of the posterior lateral line exit from the skull roof. On the other hand, the late Palaeozoic *Gnathorhiza* has totally different Y bones, and it has no lateral line canal in bone J; in addition it is unique in many other respects with which we dealt in 1990.

As has been indicated above, the second feature distinguishing *Adololopas* from other cosmine-bearing genera in the Gogo fauna is the presence of real teeth (Fig. 4). This takes it out of the group of *Chirodipterus* and *Pillararhynchus* which also occur in the Gogo fauna.

The external dermal bones of the mandible of *Adololopas* are inadequately known, preventing detailed comparison with the bones of *Chirodipterus* and *Pillararhynchus*. However, the angular (Fig. 8) has a deep and distinctive notch for the surangular, which must have had a different shape from the surangulars of *Chirodipterus* and *Pillararhynchus*. We also infer that a splenial and post splenial were present in *Adololopas*, because of the shape and position of the anterior end of the angular. Thus it would be different from *Pillararhynchus* in this respect also.

The arrangement of the scales is different from any other known Devonian dipnoan, in that they decrease dramatically in size a short distance behind the head and towards the dorsal margin. This indicates that, relative to its head size, the body was unusually short (Fig. 11). The wider significance of this feature is unknown, because so many dipnoans are known from heads only. However, *Adololopas* is much shorter in the body than the other Gogo dipnoans, *Chirodipterus, Griphognathus* and *Holodipterus* in which we have adequate body preservation. *Pillararhynchus* is more poorly known. *Dipterus* also is long bodied.

Finally, in connection with affinities, we note that *Adololopas* has a long cheek and a short snout. This type of structure was outlined by Schultze (1992), in his description of *Iowadipterus*, from the Givetian of Iowa, USA. It provided the basis on which he discriminated two types of long headed dipnoans, one type such as *Griphognathus* and *Rhinodipterus* which had long snouts, and the other such as *Iowadipterus* and *Holodipterus,* which had the post-orbital part of the skull elongated. Whereas we have no difficulty in distinguishing different types of long-headedness, we are unaware of its significance. *Adololopas* has long bones 4 and 5 and, judging from the shape of the snout and the palate, it would have been short-snouted. According to Schultze's criteria, it would be placed in the long-headed but short-snouted group. The problems raised by this assessment are dealt with below under the discussion at the end of the description.

Adololopas moyasmithae sp. nov.

ETYMOLOGY. In honour of Dr Moya Meredith Smith who has made a major contribution to the study of Palaeozoic dipnoan dentitions.

MATERIAL. HOLOTYPE: ANU49213, an incomplete specimen with part of the skull preserved. PARATYPES: WAM931.1.221, a specimen with part of the body and some skull, mandible and tooth plates preserved; and ANU49215, a small incomplete snout with the palatal and mandibular tooth-plates preserved: all from the Gogo Formation (Frasnian), Paddys Spring Valley. The two adults are so similar in structure of the tooth-plates and the cosmine on the external plates, that we see no reason to think that they are different species. The juvenile has tooth-plates in which the teeth are added at the ends of the tooth rows, successive growth of tissues at the tooth-plate margins similar to the adults, and with 6 or 7 tooth rows. All of these features are distinct from any other members of the other dipnoans in the fauna, that we can only consider all three specimens to be conspecific.

DIAGNOSIS. As for the genus.

DESCRIPTION. *Skull Roof.* Roofing bones are weakly joined at sutures, falling apart readily during etching (Figs 1, 4H,I, 5). Cosmine covers bones, except at the bone margins. Bone B is elongate, with a scalloped margin and with a pair of centrally situated pit-lines; thickening for the attachment of the median crista is restricted to the anterior half of the plate. Bone I is transverse; posterior process on I for articulation of the anocleithrum is small; position of operculum and bone 8 indicate that Y_2 must have been present, and was loosely articulated (Fig. 3C); bone Z fitted into a groove in the posterior and posterolateral margin of I. Lateral line canal enters bone I anterolaterally, runs to its centre of ossification, and then turns abruptly posterolaterally to exit into a loosely articulated Z (Figs 1, 5). Two pit-lines present on bone I, an elongate transverse one and a short posterolaterally oriented one, the two not meeting. Cartilage attaching dorsolateral crista to roof present only to the anterior part of I and extends on to posterior part of J. Anterolateral edge of I has a deep angular embayment, defining the edge of the Y_1 bone into which the lateral line passes. Bone A is transverse, roughly hexagonal, and carrying the occipital commissure; numerous sub-branches of the canal extend backwards as shown on the X-radiographs (Fig. 5); this commissure continued through bone I as a short arc. Elongate bone J is preserved on both sides and carries a lateral line canal from its centre anterolaterally to an unpreserved bone; this must have been a bone K, which was a large bone whose outline is best defined on the left side; an elongate

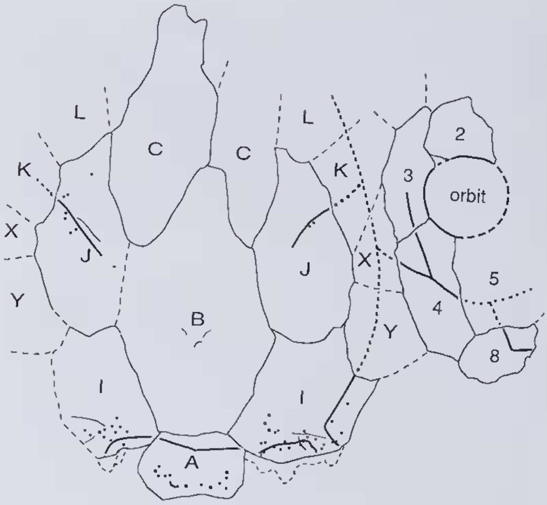


FIG. 1. *Adololopas moyasmithae* gen. et sp. nov. An outline sketch of the skull roof and part of the cheek drawn from the holotype, Fig. 4G-I. The cheek is situated in relation to the skull because the lateral line in 4 is displayed in X-rays and indicates the approximate position of the centre of ossification of X, and Y is placed to receive the lateral line from I. Scale = 10mm.

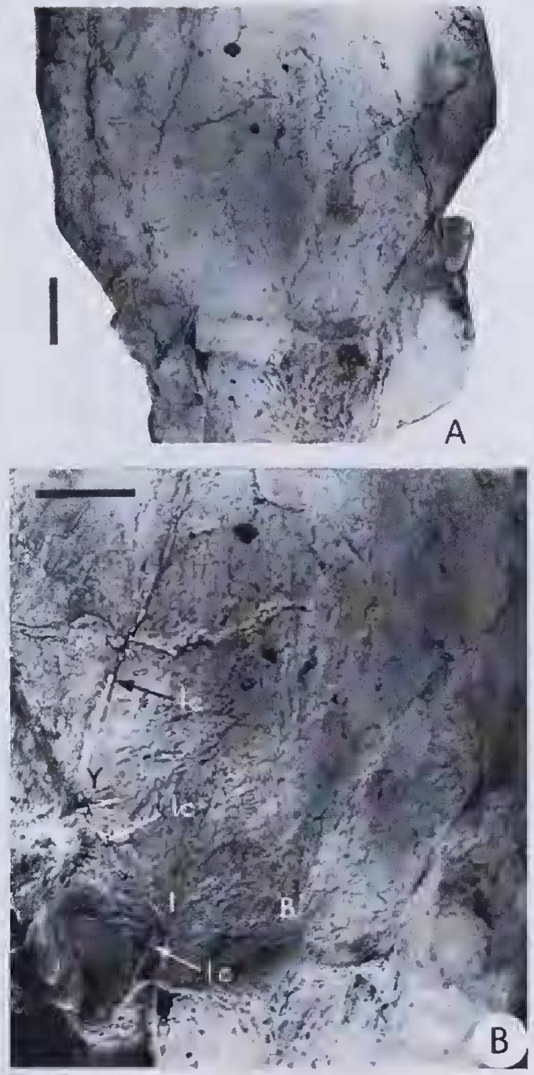


FIG. 2. *Jarvikia arctica* Lehman. This is the specimen figured by Lehman (1959, Pl. 20B). A, posterior part of the roof figured dorsally. B, enlargement of same, tilted to the right and laterally illuminated to show the lateral line canals, labelled lc. The centres of ossification of bones B, I and Y are labelled. The lines at the back of the specimen were produced by needle scratches. The bones are labelled and the canal runs off the back of the skull as shown. The extension at the back of bone I is incomplete. Scales = 10mm.

pit-line is also present on J. Bones C elongate and so shaped that any D present would have been small; other bones in front of Cs and on the cheek unknown, apart from some circumorbitals; lateral line canal present on bone 3; bone 2 short; bone 4 unusually long for a dipterid-like animal (Figs 1, 4G), extends from orbit almost to the opercular.

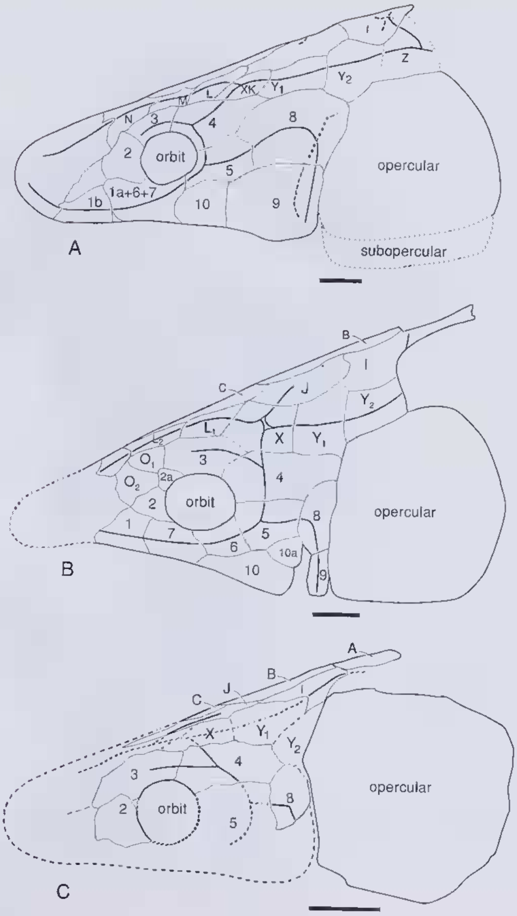


FIG. 3. Comparison between the lateral views of A, *Iowadipterus*. B, *Holodipterus*. and C, *Adololopas*. *Iowadipterus halli* is redrawn from Schultze (1992, fig. 10); *Holodipterus* is drawn from *H. (Asthenorhynchus) meemannae* (Pridmore et al., 1994). *Adololopas moyasmithae* is reconstructed from ANU49213. Note the difference in the positions of bones 4, 5 and 8.

Lateral line enters 4 from an anterodorsal rather than a posterodorsal direction, indicating that X is situated further forward relative to the orbit than in other dipterid-like animals; contact between X and J defined by projections on both sides of the specimen. Bone 8, which has been recognised by the angular bend in the lateral line and the finished edge against the opercular, is also longer than in other dipterids. Orbit 18% of length of skull from rear of B to front of C.

We have two isolated snouts, an adult from ANU49213 (Fig. 4J, K) and juvenile ANU49215 (Fig. 7A, B). Adult broad, and showing all the main features of other Devonian dipnoans of the

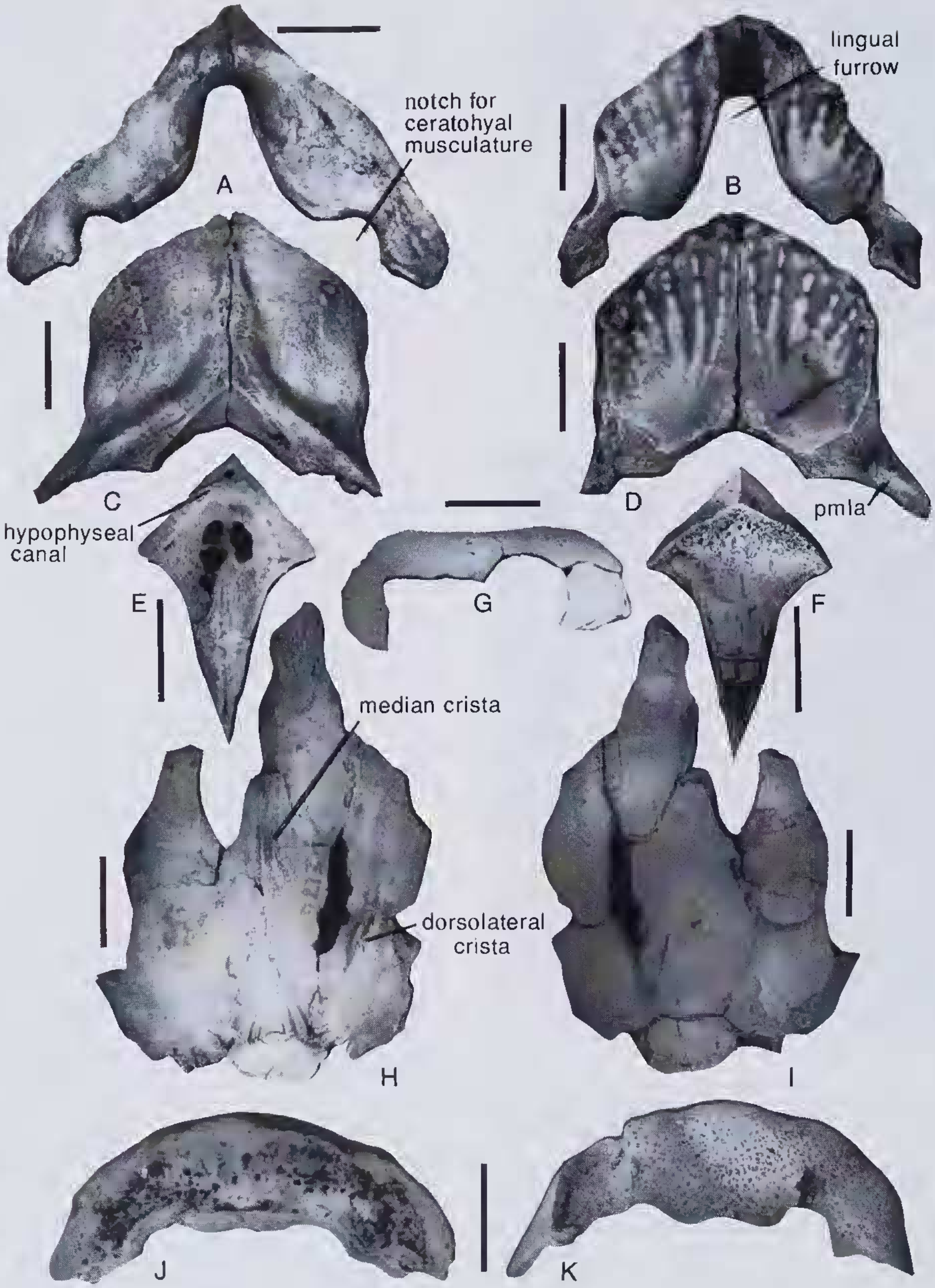


FIG. 4. *Adololopas moyasmithae* gen. et sp. nov. holotype. A, B, ventral and dorsal views of the prearticulars and tooth plates. C, D, dorsal and ventral views of the pterygoids and tooth plates. pmla = pterygoid-mandibular ligament attachment. E, F, dorsal and ventral views of parasphenoid isolated during preparation. Note the foramen in the anterior end for the buccohypophysial canal. G, lateral view of the orbit and the cheek plates. H, I, ventral and dorsal views of the posterior part of the skull roof. The left side of I is incomplete, but the bones on the right have complete edges. Note the attachment of the dorsolateral crista beneath the anterior end of bone I and the posterior end of bone J on the left side of H. J, K, posterior and anterior views of the isolated snout. Note the variation in the size of pores in the snout in K. Scales = 10mm.

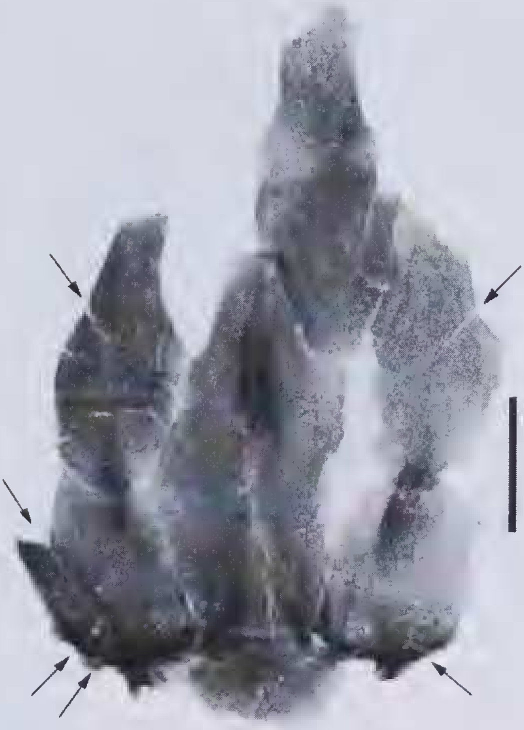


FIG. 5. *Adololopas moyasmithae.* gen. et sp. nov. X-radiograph of the posterior part of the skull of the holotype, photographed in ventral view. The entry points of the lateral lines into the bones are marked with arrows. Note also the branching of the lateral line canal in bone A (see Figs 1 & 4H). Scale = 10mm.

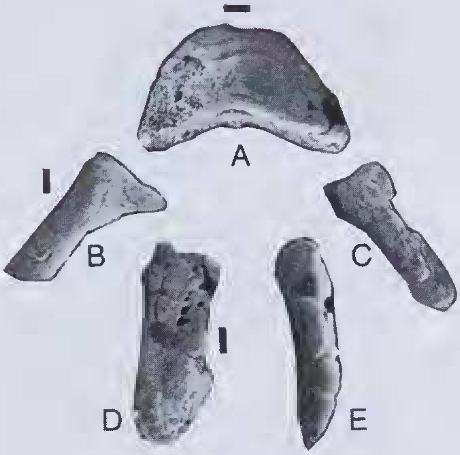


FIG. 6. *Adololopas moyasmithae* gen. et sp. nov., holotype. Isolated tooth plates from the anterior palate. A, median anterior plate showing the lines associated with new growth. B, C, pair of dermopalatine plates (in C the mesial anterior end is broken off); both show growth lines. D, E, another pair of plates of unknown origin from the same etch. Scales = 1.0mm.

dental-plated types; external nares well separated, leaving only a small edge of tissue between them and the lateral labial pit; lateral line canals defined by the enlarged pores; juvenile snouts more highly arched than those of adults.

Palate. Pterygoid thinnest towards the anterior margin, thickening gradually posteriorly; dorsal palatal process present but depressed, with a bevelled dorsal surface inclined downwards laterally and a sharp crest along its mesial margin; bevelled surface without a periosteal layer, and exposing coarser textured bone than elsewhere (Fig. 4C); a rounded ridge adjacent to the mid-line increasing in height posteriorly and turning posterolaterally along the quadrate ridge; towards the mandibular articulation the quadrate ridge becomes narrower and sharper; lateral extremity turned down sharply towards the mandibular articulation; scar for pterygo-mandibular ligament well developed, and laterally placed on the quadrate.

Included with ANU49213 are five small isolated palatal plates, one being a median anterior and two others being symmetrical dermopalatines (Fig. 6); the remaining two are possibly other anterior tooth plates (Miles, 1977, fig. 72); median plate convex ventrally and carrying incremental layers of primitive dentine, forming marginal concentric outlines (Fig. 6A); these outlines do not continue around the entire margins without breaks; however, their distribution indicates that the median plate was not in contact with the adjacent pterygoid plates; central parts of all small plates include areas within which the dentine is darkened by apparently hypermineralised dentine. Parasphenoid of ANU49213 well preserved (Figs 4E,F); anterior face high and ploughshare shaped; buccohypophysial canal situated in anterior corner, but does not open into the buccal cavity; posterior part of plate acutely triangular in outline, and with a long crest along its dorsal surface; central part of plate consisting of an open meshwork of bone.

Neurocranium unossified except at the anterior margin where tubules related to the anterior sensory systems are present.

Mandible. Mandible known from prearticulars and tooth plates of two adults and one juvenile, a small adult fragment and one adult angular. Lingual furrow of adult deep and barrel shaped (Figs 4A,B, 22A,B), slightly overhung by the tooth-

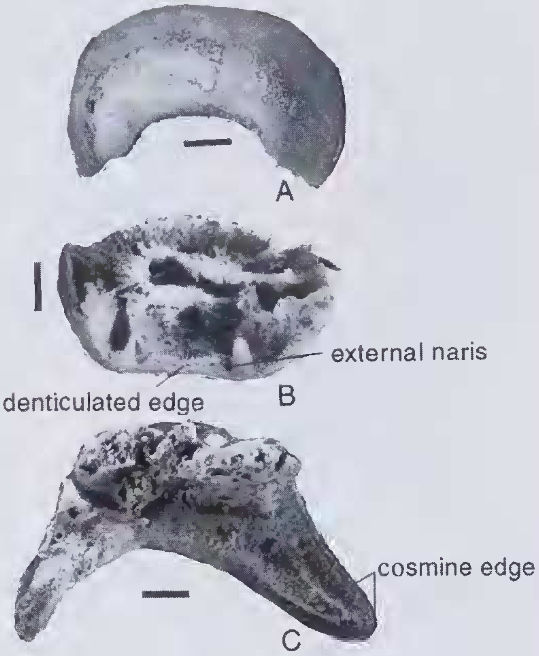


FIG. 7. *Adololopas moyasmithae* gen. et sp. nov. A, B, snout of ANU49215 in anterior and posterior views showing the high curvature. External naris labelled; pores for anterior commissure clear. C, internal view of broken dentary of the holotype. Note the edge of cosmine on the lateral and posterior edge, indicating the fact that it had no continuous bone junction with the surrounding bones. Scales = 2.0mm.

plates, and with a well rounded floor; junction between the two plates formed of bone without dentine; strong, rather sharp lateral projection of prearticular in front of the glenoid fossa (Figs 4B, 10B); pterygo-mandibular ligament attachment producing a small flange immediately medial to the glenoid fossa; between this flange and the back of the tooth plates is a deep gap for muscles connecting to the ceratohyal (Fig. 4A,B). Small isolated incomplete dentary (Fig. 7C) shows the posterior end completely isolated from the infradentaries, and having some small blisters of bone indicating that addition to the edge of the bone was taking place.

Angular, represented by an isolated external bone of WAM931.1.221, with an edge indicating that it bordered the adductor pit, and carries two lateral line canals (Fig. 8A,B); shape of this infradentary is unusual, having a deep posterior notch in which the lateral line emerges at its apex; lower lateral line enters the bone about 5mm from the posterior edge and runs forward slightly, converging on the other canal; position of infradentary bone can be determined from the opening for the adductor fossa and the large upturned surface forming the contact with the process on the prearticular in front of the glenoid fossa; shape of the surangular notch and the position of the edge of the adductor fossa, indicate that the surangular was short; shape and position of angular suggests that both splenial and postsplenial were present to occupy the space between the mid-line and the angular.

Pectoral Girdles. Two pectoral girdles, one more complete (Fig. 9A,B) from ANU49213, and the cleithrum only on WAM931.1.221 (Fig. 9C); three other smaller fragments are known. Cleithrum with a deeply concave external surface, its anterior rim standing high, sharply defined and with (Figs 9C, 11A,B) or without (Fig. 9A,B) a large number of pustules; posterior half of external surface covered with moderately developed rough surface features; ventral extremity acute and with an angular excavation for the articulation of the clavicle; branchial lamina standing at a high angle to the external lamina, concave on its anterior face, and carrying a number of sharp projections into this concavity; dorsal

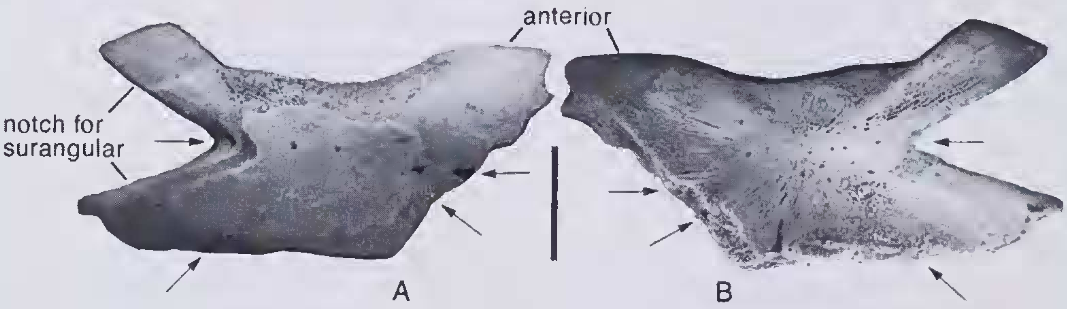


FIG. 8. *Adololopas moyasmithae* gen. et sp. nov. A, external and B, internal views of an isolated angular bone from WAM931.1.221. Position of mandibular and oral canals marked by arrows. Notch for surangular with a margin unaltered by etching. Opening for adductor muscles obvious at top of photograph. Scale = 10mm.

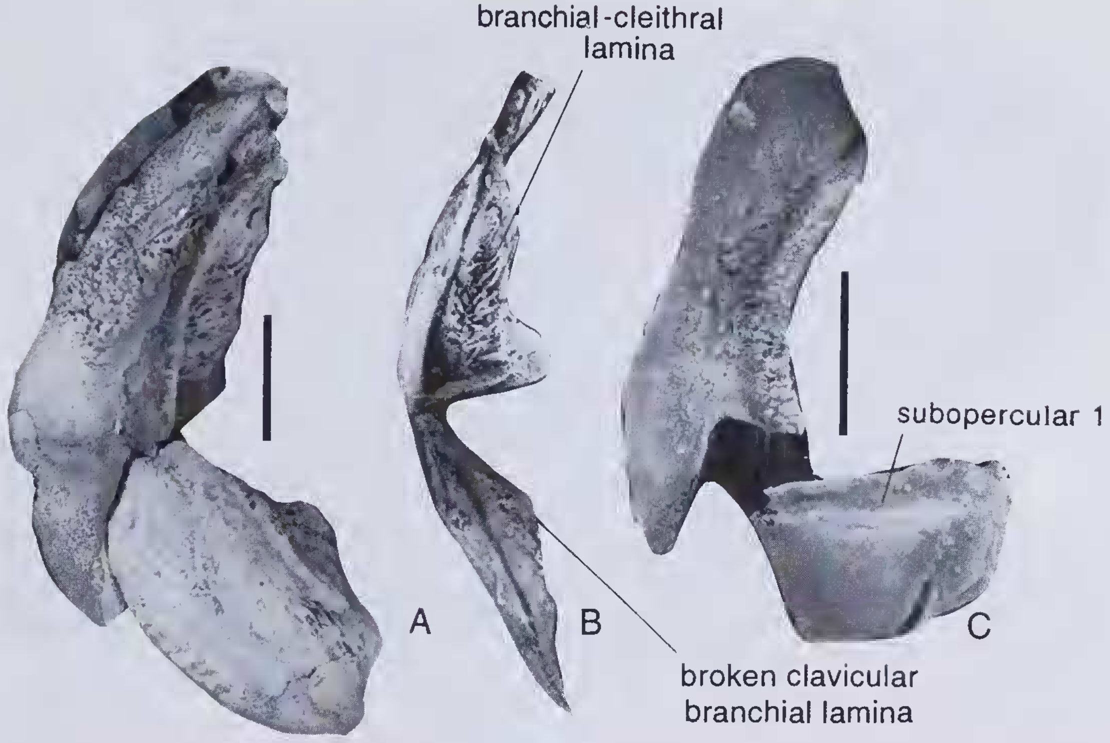

branchial-cleithral lamina
subopercular 1
A
B
C
broken clavicular branchial lamina

FIG. 9. *Adololopas moyasmithae* gen. et sp. nov. A, B, lateral and anterior views of an incomplete right pectoral girdle of the holotype. In A and B the branchial lamina on the clavicle is incomplete. C, cleithrum and the subopercular 1 of WAM931.1.221. Note the difference in ornamental pattern between this specimen and that of A. Scales = 10mm.

edge of lamina meeting the anterior edge of cleithrum about 8mm short of dorsal edge; ventral edge of branchial lamina thickened and bearing a distinct groove for the articulation of the clavicular branchial lamina. Clavicle with a much less concave external lamina and a weaker anterior rim than the cleithrum; ornament well developed on the anterior rather than the posterior half; ventral end of external lamina with a cutaway edge that continues up into the branchial lamina, producing an over-lapped surface presumably for the interclavicle; branchial lamina incomplete, but extending nearer to ventral edge than in *Chirodipterus australis;* originally it continued up to meet the cleithral branchial lamina along its entire length.

Operculars and Gulars. Opercular subquadrate in outline; leading edge almost straight ventrally (Fig. 10A,B), but turned posterodorsally on the upper edge; in anterior view, dorsal part of operculum bent medially; anterior edge of this inturned part of bone abutts the posterior edge of the Y2 bone; the inward turning of the operculum demonstrates that the rotational edge lay ventral to the upper edge of bone 8; this articulatory edge with slight overlapped margin, indicating the position of movement against the skull; posteroventral edge also slightly truncated; dorsal edge also overlapped; surface with strong Westoll lines.

Subopercular 1 with a strongly overlapped dorsal edge and a slightly ventrally curved ventral edge (Figs 9C, 10B); remainder of surface covered with cosmine apart from marginal resorption. Subopercular 2 not well-known, only partly exposed (Fig. 10B), but with overlap edges on both dorsal and ventral edges.

Principal gulars (Fig. 10B) generally ovate in outline, but with a strong point anterolaterally; about 18mm long and 18mm wide; anteromesial edge with a long undivided overlap which indicating a large median gular; lateral overlaps not completely clear, but indicating a submandibular and possibly a lateral gular; three Westoll lines on the surface; a transverse pitline 4mm long situated anteromesially on the plate.

Pectoral Fins. External ornament of the right pectoral fin partly preserved on WAM931.1.221 (Fig. 11A,B); individual scales small, cosmine

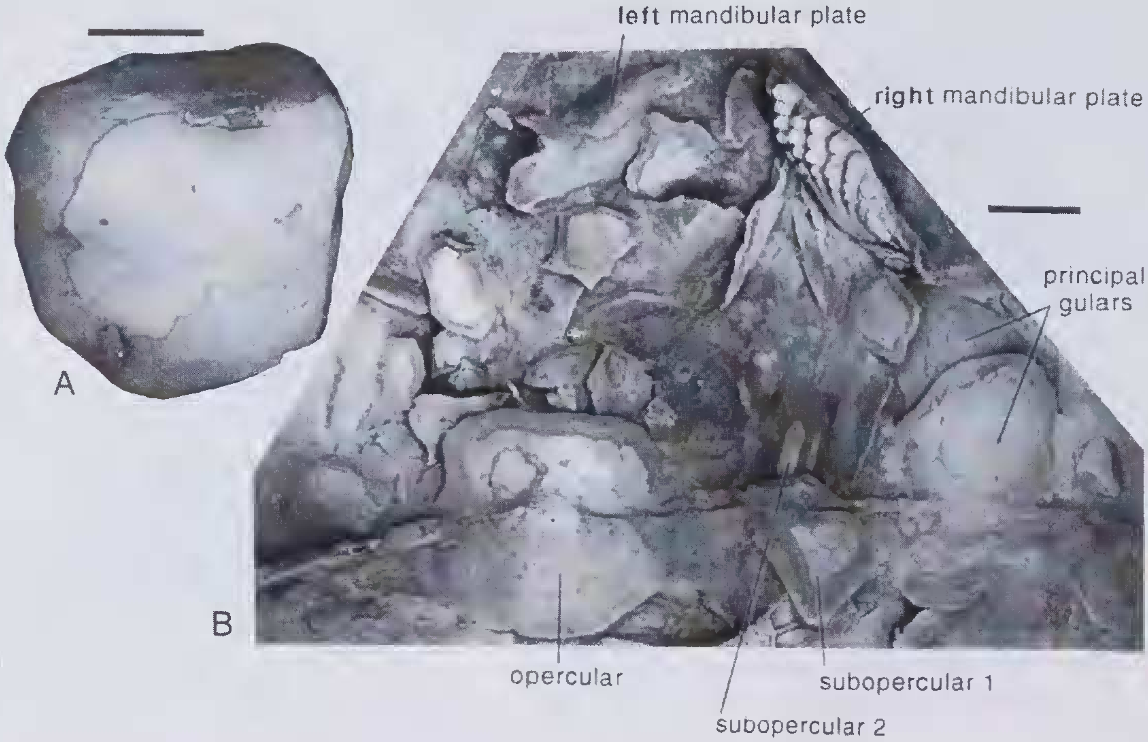


FIG. 10. *Adololopas moyasmithae* gen. et sp. nov. A, an isolated operculum of holotype; anterior to the right. B, WAM931.1.221, anterior part of specimen showing opercular, gular, subopercular 1 and 2 and mandibular plates. Scales = 10mm.

covered but with a small overlapped edge on some individuals; preserved part of fin 22mm long; occasional scales preserved on the inside of the limb (Fig. 11B); individual scales highly variable in outline; overlaps slight; probably only two or three rows of scales down the midline of the fin, but there may have been a smaller row on each side; no rays preserved.

Scales. Scales thin, cycloid in shape, and almost equidimensional in outline; inner surface with concentric growth lines; exposed surface with cosmine; size of scales decreases rapidly in both dorsal and posterior directions; on the flanks only 100mm behind the head, the length of the cosmine cover is only half of the forward scales (Fig. 11A); scale overlap is large (Figs 11A, 12). Scales immediately posterior to the cleithrum show no sign of cosmine (Fig. 11A,C). Like the cleithrum itself, they must have been buried beneath a thin layer of soft tissue.

DESCRIPTION OF TOOTH-PLATES. *Macromorphology of Juveniles*. At the early growth stages, the palatal plates show very narrow bands of shiny (probably enamel-covered) dentine along the posteromesial edge, and these abruptly expand to form large flat surfaces anteromesially (Figs 13, 14). These bands are continuous around the posterior edge of the plate to the lateral margins where the inner ones progressively disappear, or can be faintly traced turning inwards between the teeth. The two outermost bands are quite clearly in two discontinuous units (Fig. 13C,D). The posteriormost one is replaced by another band which continues around the anteior margins of the plate, and carries the succession of teeth upon its surface. The band swings back between the teeth on the anterior edges (Figs 13A, 14C). There is no precise correspondence between the marginal bands and the addition of new teeth (Figs 13A,B). It is obvious that six teeth are added while four marginal bands were growing (Fig. 13B). The situation on the right plate is not so clear because of weathering, but the bands of tissue running across the plate surface are well marked (Fig. 13A). There is no sign of clear resorption and replacement of any bands, but more mineralised dentine of the plate has grown into some of the inner bands in places.

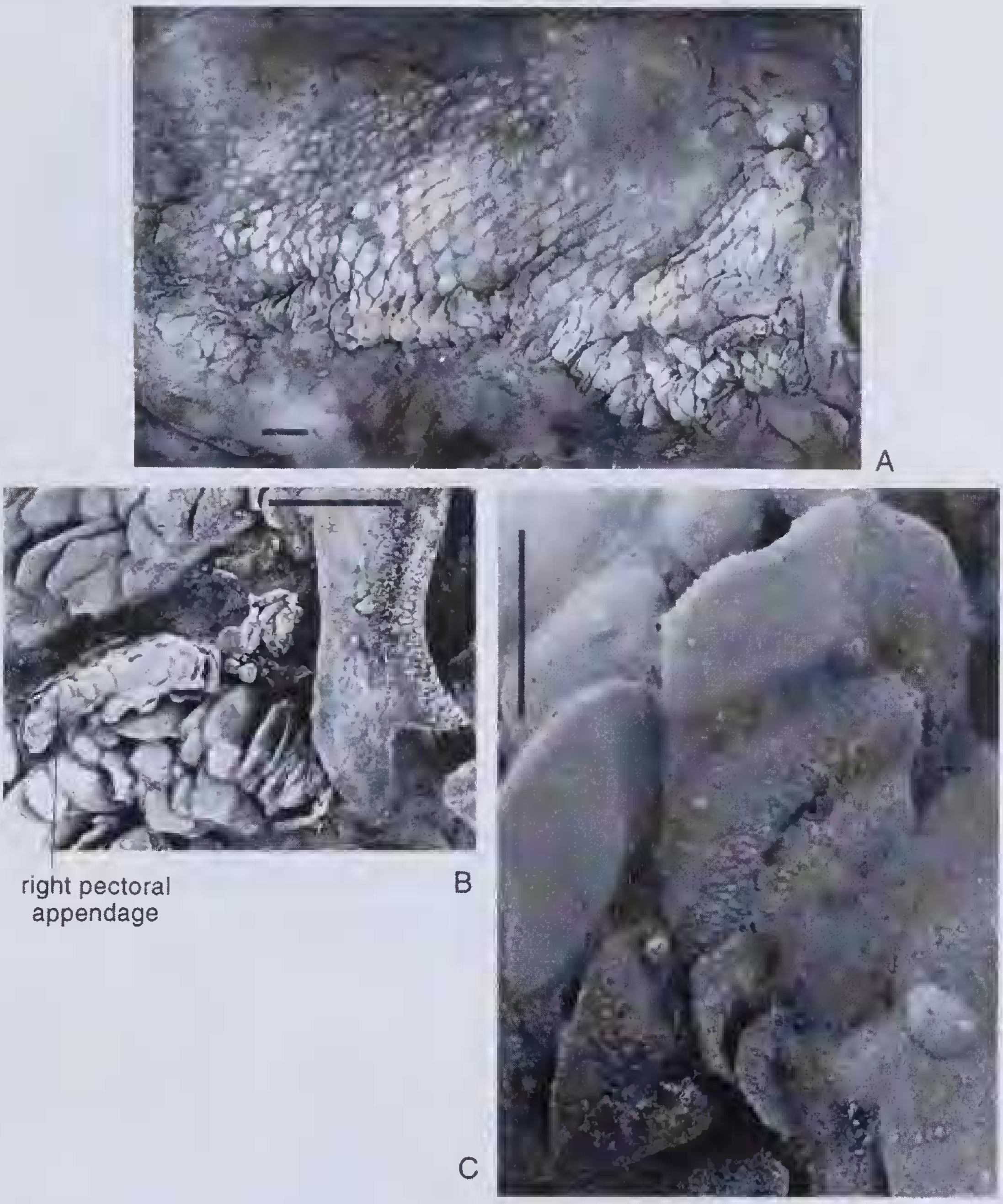


FIG. 11. *Adololopas moyasmithae* gen. et sp. nov. A, body of WAM931.1.221; note the rapid reduction of scale size from front to back and from ventral to dorsal sides. B, cleithrum and right pectoral appendage; note the ornament on the cleithrum. C, enlargement of scales immediately behind the cleithrum; note that the more anterior scales lack cosmine and are covered with pustules. One cosmine-bearing scale in particular has pustules along its posterodorsal edge. Scales A-B = 10mm; C = 5mm.

The lingual face of the juvenile mandibular plates stands almost vertically, and is covered by a sequence of four layers of enamel-covered dentine, the most recently added of them being ventral and the oldest against the plate proper (Fig. 15C,D). In the lingual furrow they have a distinctive shape; their ventral edges are slightly curved except towards the anterior end where they bend

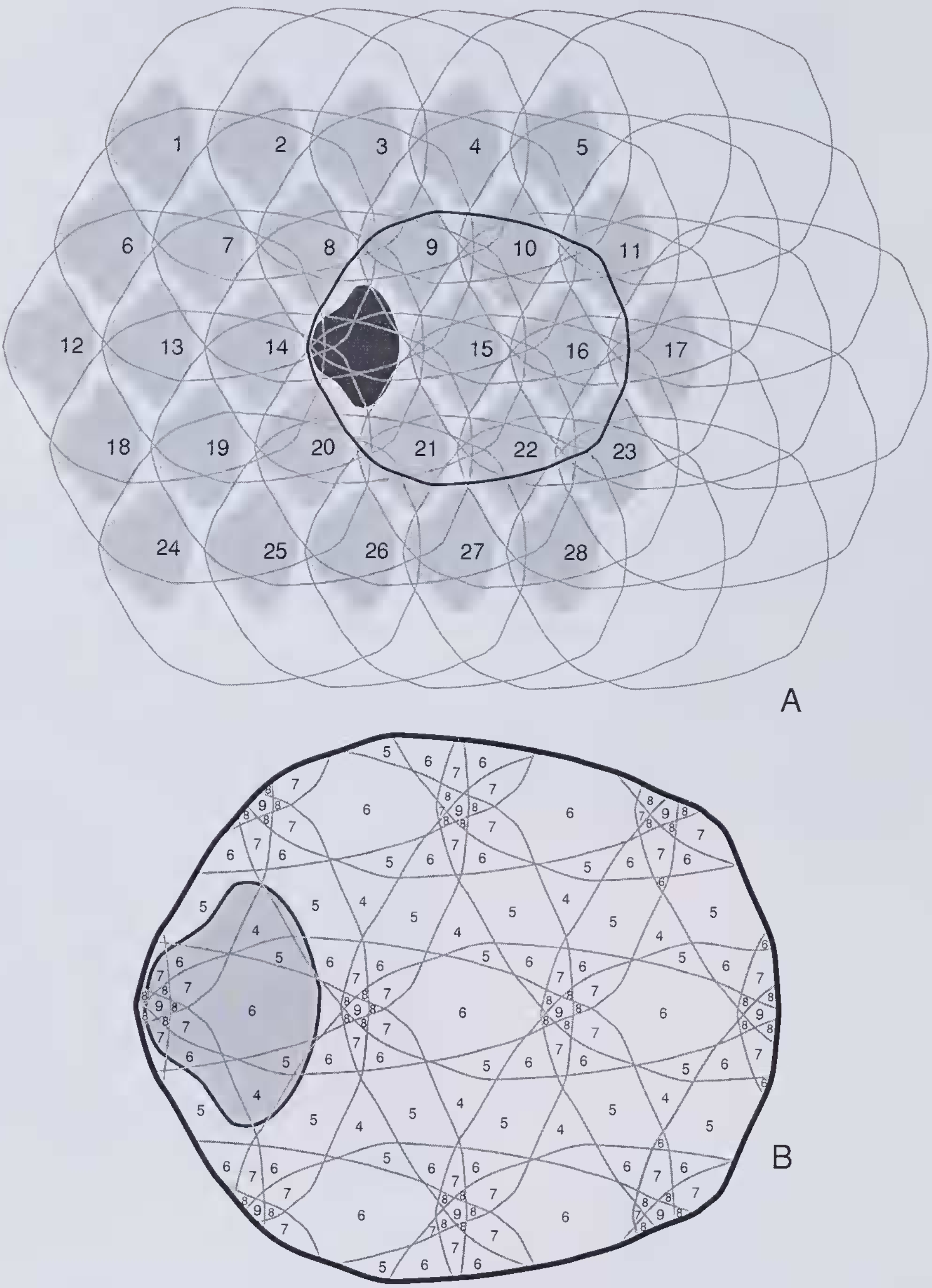


FIG. 12. *Adololopas moyasmithae* gen. et sp. nov. A, computer reconstruction of lateral flank scales drawn on the basis of one scale in dark outline in the centre of the illustration; cosmine coloured black. Cosmine of adjacent scales grey, and surrounded by open areas which indicate bone covered with soft tissue. Twenty eight scales, which potentially were in contact with the main central scale, have been drawn in. B, computer reconstruction of lateral flank scale, cosmine-covered area in light grey, with the estimated pattern of edges of overlapping scales. Numbers refer to the potential number of overlapping scales at particular points on the scale.

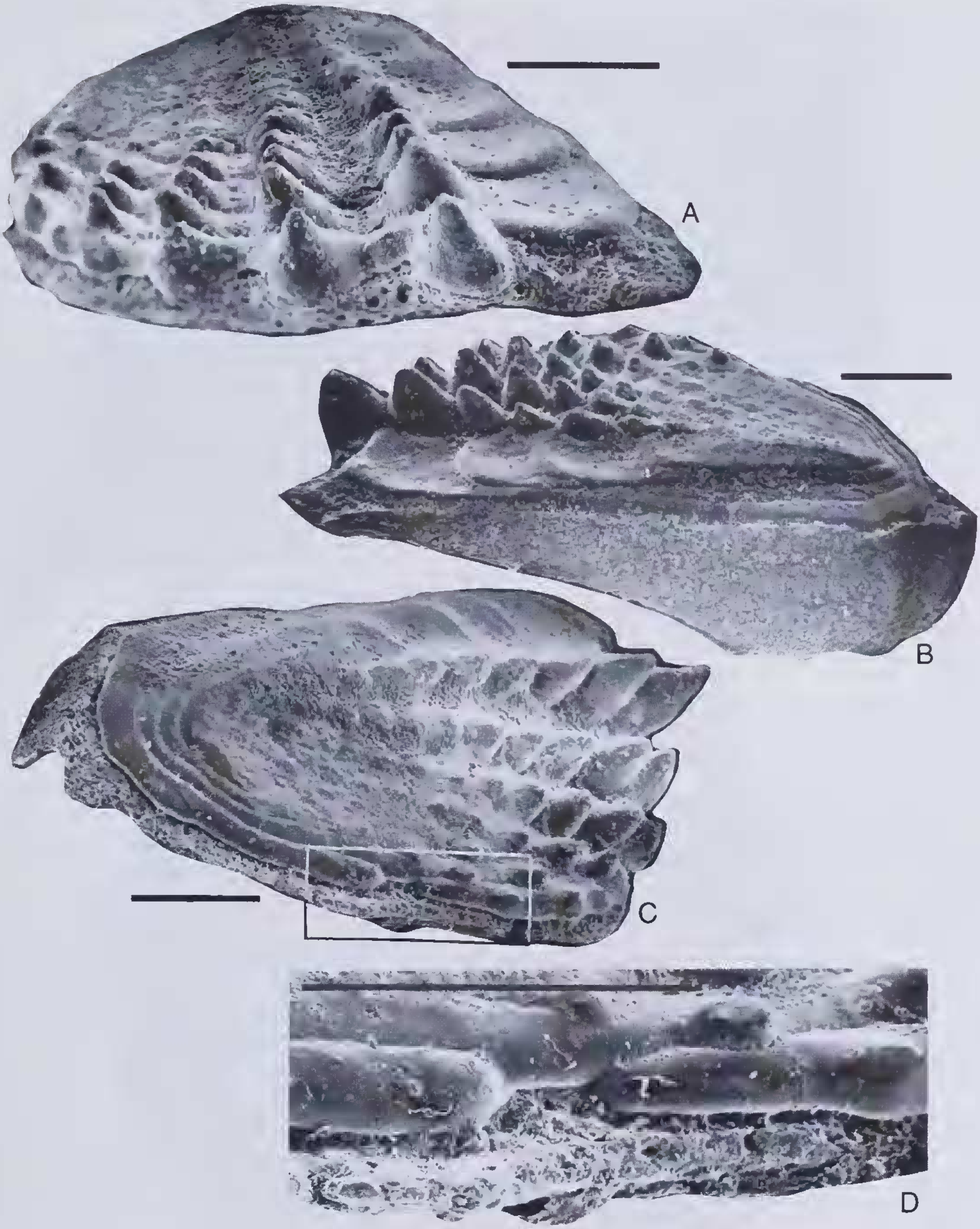


FIG. 13. *Adololopas moyasmithae* gen. et sp. nov. Palatal-tooth plates of the juvenile, ANU49215; right palatal plate (from top to bottom) in anteroventral, medial ventral, ventral and marginal views. A, note the marginal teeth lying directly on bone, and layers of enamel-covered tissue adjacent to the mid-line and bending inwards behind the marginal teeth. B, C, bands of enamel-covered material around the posterior medial and lateral edges, show particularly well. D, shows the break between the posterior band of tissue and the tooth bearing band in front. Scales A-D =1 mm.

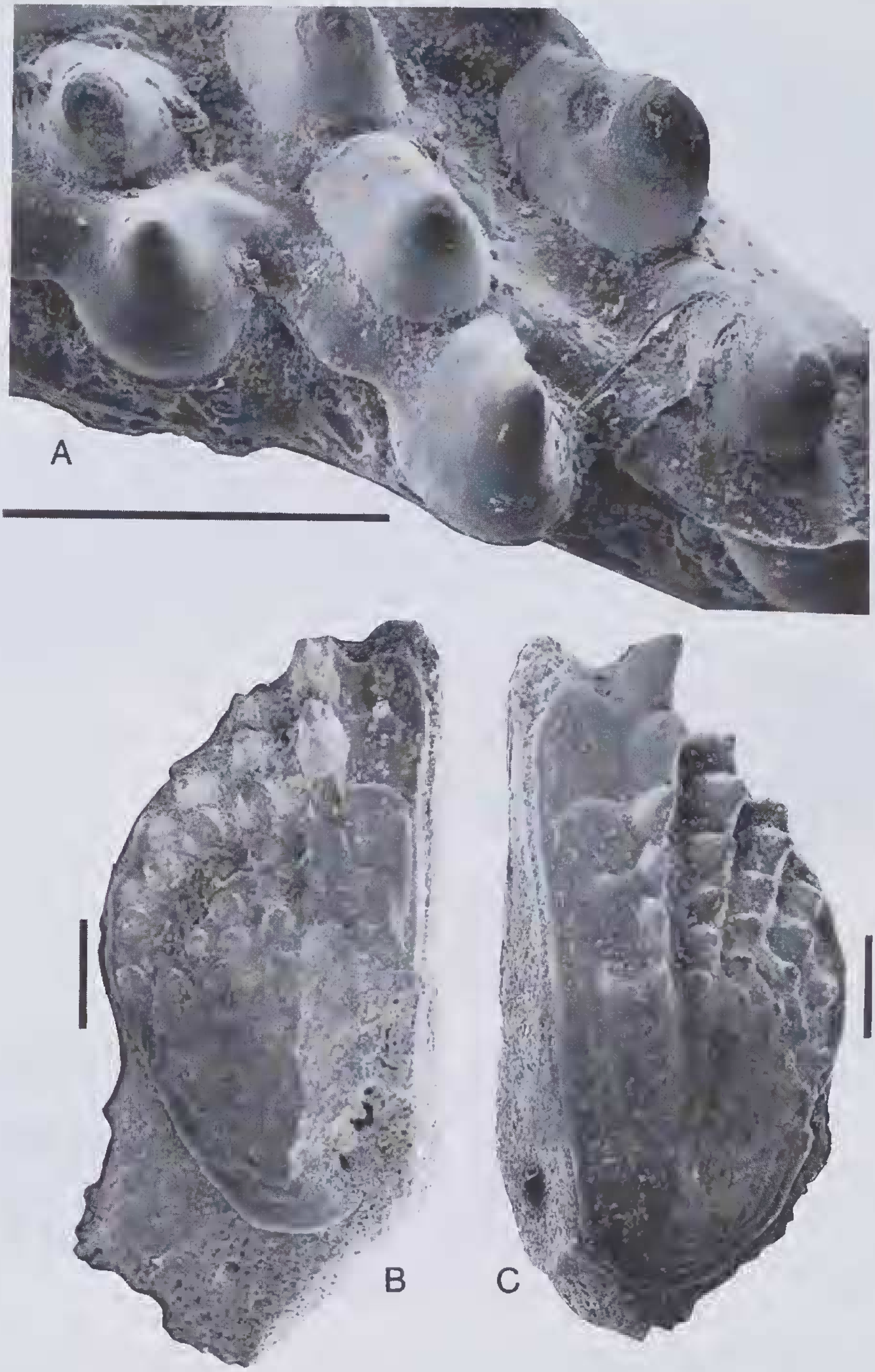


FIG. 14. *Adololopas moyasmithae* gen. et sp. nov. Palatal tooth-plates of the juvenile ANU49215. A, marginal view showing teeth and marginal bone. B, C, two palatal tooth plates of the one specimen. B, slightly destroyed by erosion on the original specimen. Scales = 1mm.

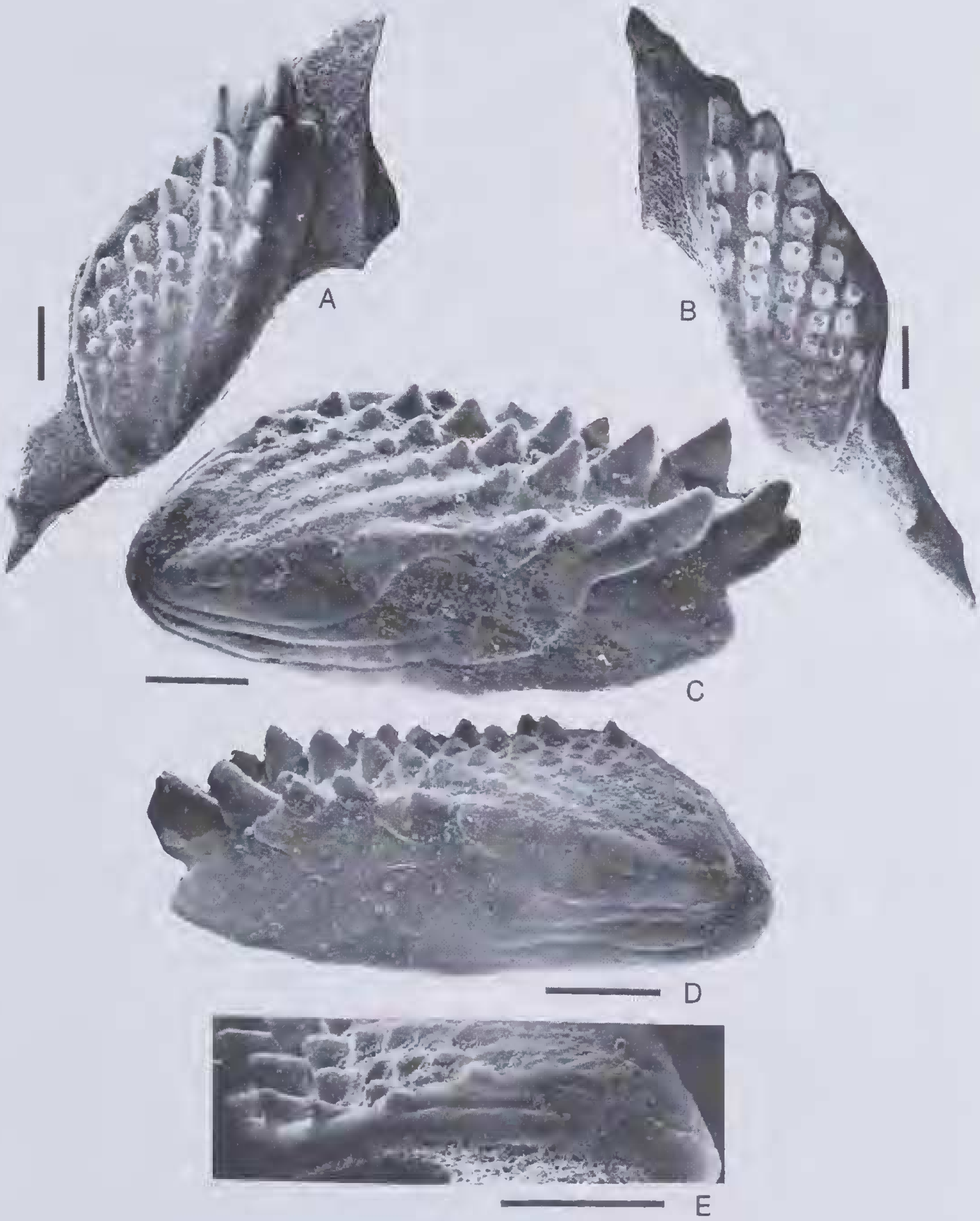


FIG. 15. *Adololopas moyasmithae* gen. et sp. nov. Mandibular tooth-plates of the juvenile ANU49215. A, B, dorsal views of two plates; note the exposed bone in the mid-line. C, D, lingual views of the left and right plates showing the enamel-covered bands. E, view of the posterior lateral edge of A. Scales = 1mm.

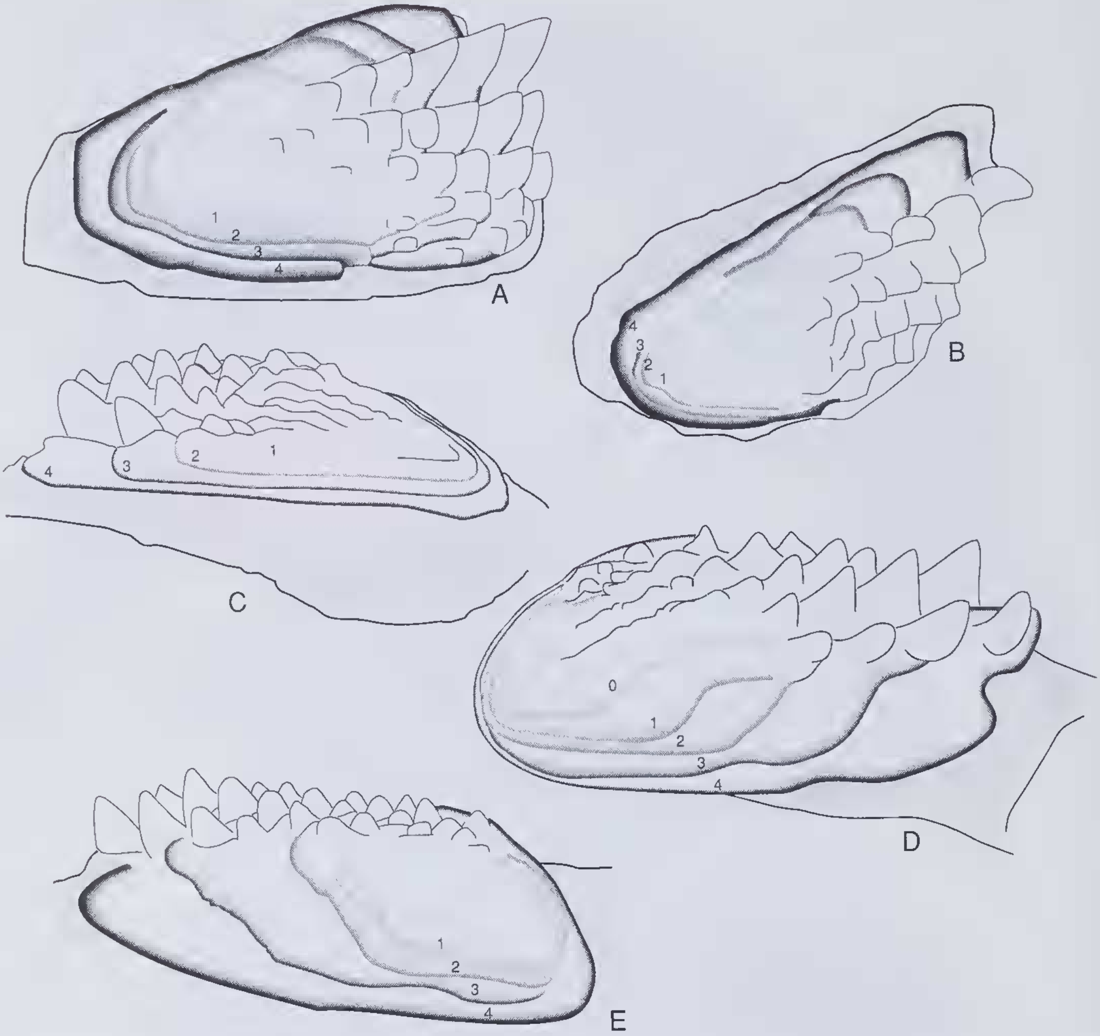


FIG. 16. *Adololopas moyasmithae* gen. et sp. nov. Outline drawings of the juvenile specimens of tooth plates in Figs 13-15. A-C, three views of the left palatal plate showing the marginal bands numbered 1-4. D, E, lingual views of the left and right mandibular plates, again showing the marginal bands 1-4.

sharply upwards and then loop forwards on to the flanks of, or around, the last-formed tooth. This gives the superficial impression that a new layer is formed contemporaneously with the addition of a new tooth, but that is not correct. As is shown by an examination of the anterolateral margin of the plate, new teeth are added directly on to bone and then a layer of dentine was deposited around the distal edges of the teeth. These bands were continued around the posterior margin of the plate, though some of the earlier formed ones were overlapped by the later ones. Only the last formed continues around the lateral edge of the plate, and it turns in behind the distal tooth on the third row and then continues in the furrows proximal to the distal tooth on the second and first rows.

Macromorphology of Adults. The adult *palatal* tooth plates of two specimens are known. The better preserved one (Figs 4C,D, 17A-D), has 6 well-formed rows of teeth with an indication of a seventh. In ventral view, the posteromedial edge of the plates against the median suture shows the remnants of four dentine bands (Figs 17A, 21). These bands have resorbed posterior edges, and are ingrown to various extents by columns of dark, apparently hypermineralised, dentine. The dark bands appear as slightly darker bands within the white dentine. These bands of tissue narrow anteriorly for about 4mm, where they become indistinguishable. Anterior to them, the surface of the plate is formed by bony tissue along the median edge of which there are few narrow elongate blisters of dentine which butt up against the mesial side of the two most anterior teeth (Fig. 17D). These blisters become larger anteriorly.

On the posterior margin of both plates three bands of dentine can be distinguished, the inner one strongly ingrown with columns of hypermineralised dentine; the outer one shows an irregular edge, indicating deposition not long before death. This outer band also contains a small number of pores as in *C. australis* (Smith & Campbell, 1987, pl. 4, figs 24-26). The lateral margins of the plate (Figs 17B,21) have a single narrow band of dentine that continues forward to the fifth or sixth row of teeth where it turns inwards forming a ridge in each furrow proximal to the most distal tooth in each row. This most distal tooth on each row lies directly on bone (Fig. 17B,C), and the concentric layer of enamel-covered tissue abutts the inner edge of the distal teeth, indicating that it did not form a continuous layer around the edge of the plate.

Preparation of the paratype has allowed the dentine to fall free of the pterygoid (Figs 18A,B, 19A,B, 20A-C). A basal pulp cavity is continuous longitudinally beneath the tooth-bearing rows, except at the distal ends where there is bone beneath the outer edge of the last-formed tooth. Bone lies at the distal ends of the teeth and extends slightly beyond it (Fig. 17B,C). Pterygoid bone joins the tooth plate between the tooth rows in thin bands. This bone joins bone and coarse dentine that lies between the rows of teeth on the occlusal surface (Fig. 17B). More detail of this arrangement is described below in the histology section. Along the lateral face of the plate the bone of the pterygoid also makes a continuous junction with the dentine (Fig. 19A). Although the broken specimen is not completely clear, bone also meets the coarse dentine medial to the innermost tooth row. The breadth of this bone increases posteriorly. Beneath the thick solid dentine part of the plate forming the heel, the dentine is braced against the pterygoid by irregular discontinuous masses of bone, which become more closely spaced posteriorly where the dentine thins out (Figs 18-20).

The mandibular tooth-plates are convex, and contain six rows of teeth (Figs 4B, 22B,C); in each row, the last five or six teeth can be distinguished; individual teeth have the same form as those on the palate. The plate is convex, and the most distal tooth lies directly on bone (Figs 10B, 22B,C). The left side of ANU49213 shows the growth series of tooth structure (Fig. 22B). Along the left side of the plate is a continuous layer of enamel-edged tissue which runs forward to, and around, the last formed tooth in the sixth row (Fig. 22B). At that point it turns inwards to form a boundary edge proximal to the distal tooth in the fifth row. It then continues across the plate inside the distal tooth in each row until the median row in which there are two teeth distal to it (Fig. 22B). The bone on which the distal tooth sits is coarse at the base and fines up to the tooth base. As can be seen from the surface, the bone extends inwards between the rows, and becomes progressively more ingrown by dark dentine proximally. Laterally the same type of tissue extends proximally between the sixth row of teeth and the marginal ridge.

A broken mandible (Fig. 22A), shows well the layers of reparative dentine along the lingual surface. These are in short sections in about four layers. Those at the dorsal edge are slightly eroded, and at the ventral edge are fresh, being the latest ones formed. As can be distinguished in this photograph, the bones lie below the dentine and form a slightly concave surface in the lingual furrow.

HISTOLOGY OF ADULT TOOTH-PLATES

DISTAL TOOTH. *Enamel and Pallial Dentine.* The tooth plates add considerably to our understanding of the Late Devonian evolution of the marginal growth mechanisms, the pulp cavities and pulp canals, and the distribution of the various types of dentine. Vertical sections along the tooth rows (Fig. 23A,C) show a continuous basal pulp cavity which extends to the inner edge of the most distal tooth. At that point, the bone runs onto the outer edge of the second last tooth, making a firm connection between the bone and the outer edge of that tooth (Figs 23A,C, 24A,B, 25A,B).

The distal tooth is covered with enamel except on the tritural surface where it has been worn away. The enamel layer extends over the outer surface of the distal tooth terminating deeper than the basal pulp cavity (Figs 24A,B, 25A,B, 26D). Beneath the enamel is a layer of dentine of variable thickness, dark in colour on SEMs, but light in transmitted light (Figs 23A-D, 24A-D, 25A,B, 26A-C,E,F). This is the pallial dentine layer, or mantle dentine of Weidenreich (1925) and Lund et al. (1992), which is found in all Palaeozoic dipnoans. For our usage of pallial dentine, see Campbell & Smith (1987: 166). Some of the pulp canals in the pallial dentine are continuous with

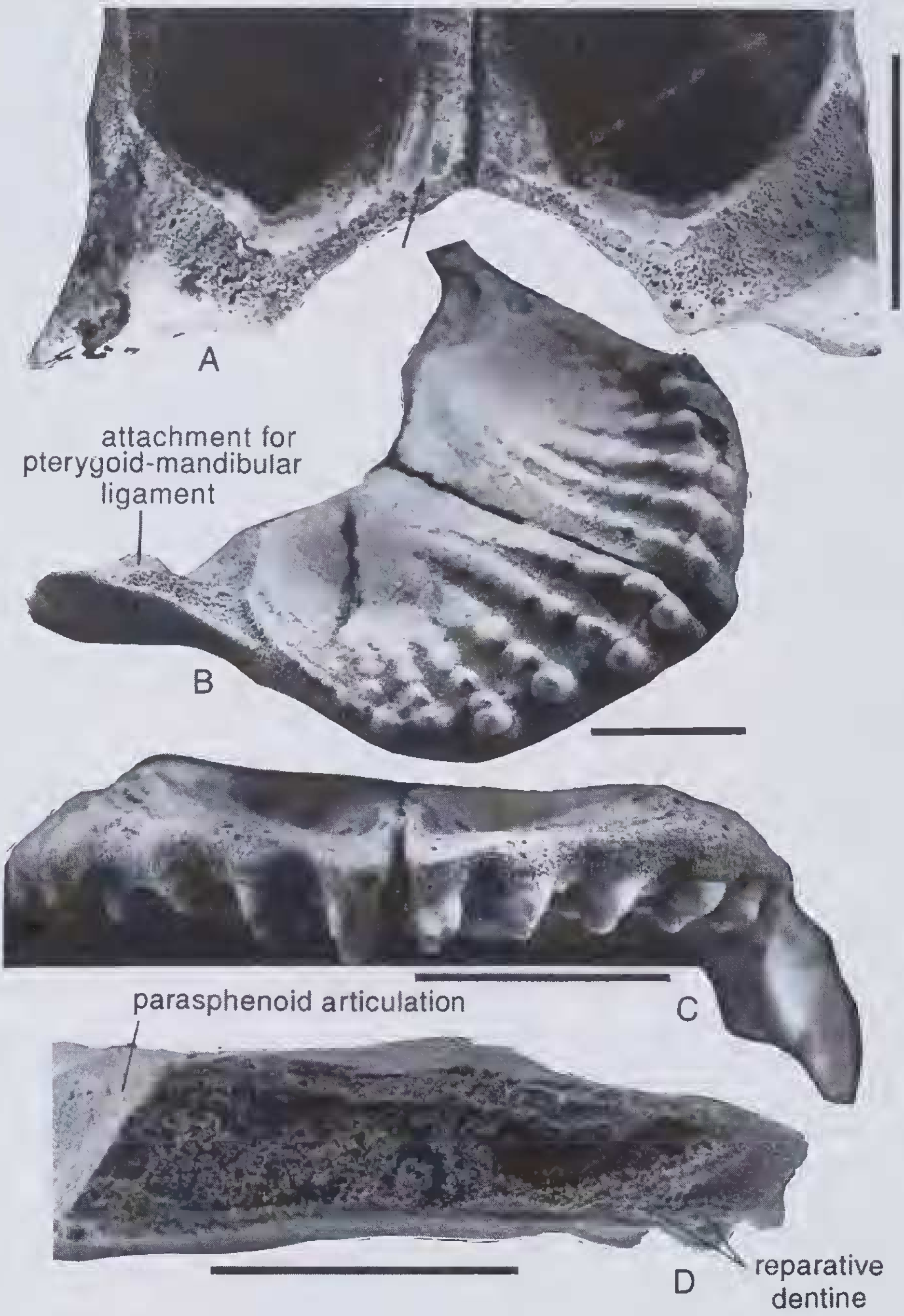

A
attachment for pterygoid-mandibular ligament
B
C
parasphenoid articulation
D
reparative dentine

FIG. 17. *Adololopas moyasmithae* gen. et sp. nov. Pterygoid tooth-plates of the holotype. A, view of the posterior part of the palatal plates; note in particular the primitive dentine around the posterior edges of the plates and the successively generated layers of dentine along the median-posterior edges of the plates (arrowed). B, oblique view of the plates. C, anterior end of the same plates showing the teeth lying directly on bone and having enamel forming only around the teeth themselves; note also the down-turned part of the plate to the mandibular articulation. D, medial view of the left tooth plate which has been separated from the other plate; showing the articulation of the parasphenoid and the two small blisters of primitive reparative dentine towards the front of the plate. Scales = 10mm.

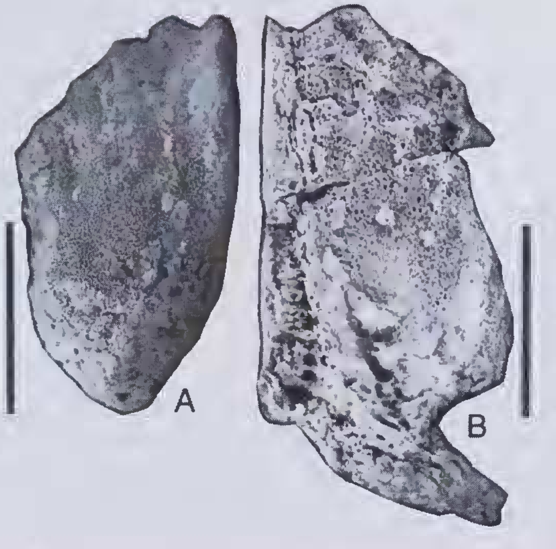


FIG. 18. *Adololopas moyasmithae* gen. et sp. nov. An isolated left pterygoidal plate of WAM93.1.221. A, The dorsal surface of dentine part of the plate showing the bases of the pulp canals. B, bone from which the dentine has been separated; A and B will fit together; B shows the positions of the pulp canals adjacent to the bone, and the white patches are the remains of the bone joining the pterygoid to the dentine plate. Note the abundance of bone attachment under the heel of the plate. Scales = 10mm.

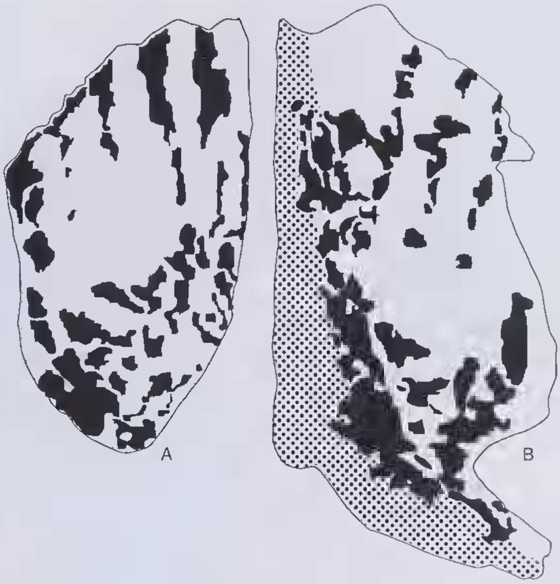


FIG. 19. *Adololopas moyasmithae* gen. et sp. nov. Drawing of Fig. 18, showing the points of contact between the dentine and the pterygoid bone in black. Note that the two surfaces do not fit together because when the two were separated, the bony contacts separated part to one side and part to the other. Fine stipple refers to surface without attachment between the bone and dentine, and coarse stipple to parts of pterygoid not joined to dentine.

those of the core dentine of the tooth, but others are directly connected with the underlying tissue on the inside of the tooth. We refer to this as pedestal dentine, and it will be discussed below (Figs 24A-D, 25A-B, 26C-D). At their tips, the pulp canals in the pallial dentine branch to form a thicket of dentine tubules which are not always obvious (Fig. 26F). Under crossed polarised light, this layer has a different pattern (Figs 24B,D, 25B, 26A) from the remainder of the dentine.

The Core Dentine. In thin section, the core of the distal tooth is made of dark brownish tissue which forms a dense mass. It appears in weathered surfaces as a dark material, and it is hard wearing; so to some extent it must be hypermineralised. In it the pulp canals are slightly bent, but they form continuous structures from the basal pulp cavity to the base of the pallial dentine (Figs 24A-D, 25A,B, 26A,B). The hypermineralised dentine was formed directly from the basal pulp cavity. Occasional branching of the pulp canals is observed, and interconnecting canals are common. Extending out at right angles to the canals are abundant dentine tubules (Figs 24A, 25A, 26D) which are more obvious nearer the pulp cavity, although more occlusally in the tooth they are occasionally visible, where they are narrower. Tubules are well shown on some SEMs where they are delicate structures which branch repeatedly away from the canal and form a meshwork (Fig. 28B). As is shown in Fig. 27B & C, the crystal fibre bundles composing the dentine make a basket weave throughout the tissue (Smith, 1984), such as occurs in petrodentine. They are similar to the structure described by Campbell & Smith in the teeth of *Holodipterus gogoensis* (Campbell & Smith, 1987). We do not have enough material to cut horizontal sections through each tooth to determine the birefringence of the crystal fibre bundles. The abundance of tubules throughout the tissue indicates that it is not typical petrodentine, though it may be an intermediate stage in the evolution of petrodentine. In fact, it is a compact structure for which we can find no acceptable term among the many available ones. We will therefore refer to it as ‘a compact dentine’ in generic terms, not intending that this be taken as a new term for dentine morphology.

Pedestal Dentine. Between the pallial dentine and the compact dentine of the distal tooth, is a layer of dentine which has pulp canals which are very

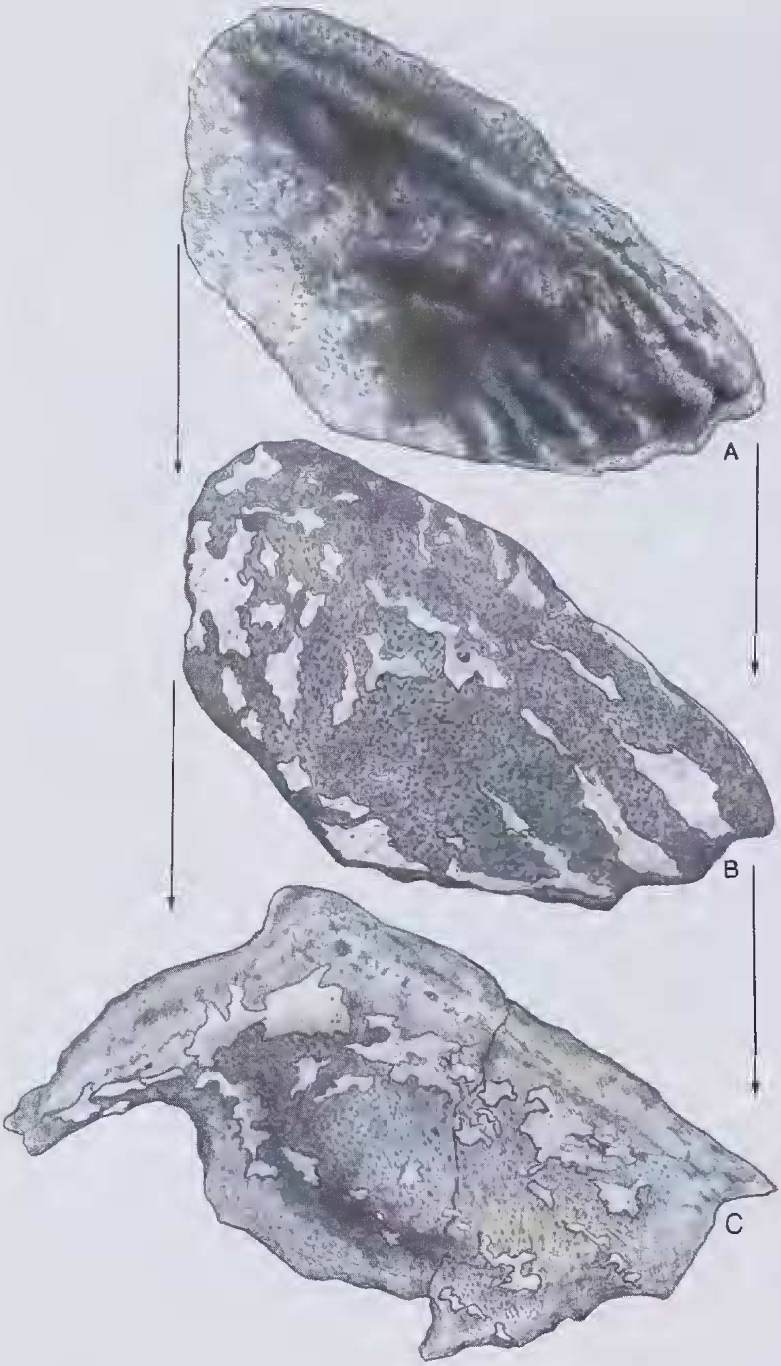


FIG. 20. *Adololopas moyasmithae* gen. et sp. nov. A, occlusal view of pterygoidal tooth-plate. B, dorsal view of tooth-plate, but reversed so that it is in the same orientation as the occlusal view, to show the alignment of the bony patches of the underside of the tooth plate as they correspond to the gaps between the surface ridges. C, bone of the pterygoid to show the surfaces to which the dentine plate was attached. Arrows indicate points of the superimposition of dentine on bone. Note that B is a mirror image of the underside of A, and it represents the joining suface with C. Arrows indicate the points of superimposition.

distinct in some sections and weaker in others. This dentine is well shown in Figs 24A,C, 25A,B, 26A-D. It has the same colour as the underlying bone. It is always better developed on the inner edge of the distal tooth than the outer. The pulp canals in this dentine do not connect with the basal pulp cavity at their bases, but towards the occlusal edge of the tooth they are connected into the pallial dentine (Figs 24A, 25A, 26B-D). At the base they seem to grade into bone, which is distinguished by osteocyte spaces. Dentine tubules, coming off pulp canals, are not obvious in this dentine, but occasionally they can be detected. In Figs 24A,C, 26A-C this dentine is in contact with the core dentine of the previous tooth, and cuts into the dentine pulp canals of that tooth. As seen in Figs 23A,C, 26A-C, this dentine is lost, presumably by resorption, and it is not visible in any preceding tooth.

Some pulp canals extend into the tissue between the distal tooth and the preceeding tooth (Figs 23A,B, 24A-D, 26A-C). As can be seen in Figs 24A-D, 26C, which are optical photographs, and Figs 23A-B, which represents the SEM reproduction of the same feature, this layer of the most distal tooth lies occlusal to the enamel and pallial dentine of the second last tooth. The enamel (Fig. 23B, 24A-D) is left embedded in the matrix and it surmounts the bone on which it lies. The sharp boundary between this layer, and the underlying compact dentine which forms the core of the tooth, is well shown on Figs 23B, 26C. The SEM shows how the compact dentine does

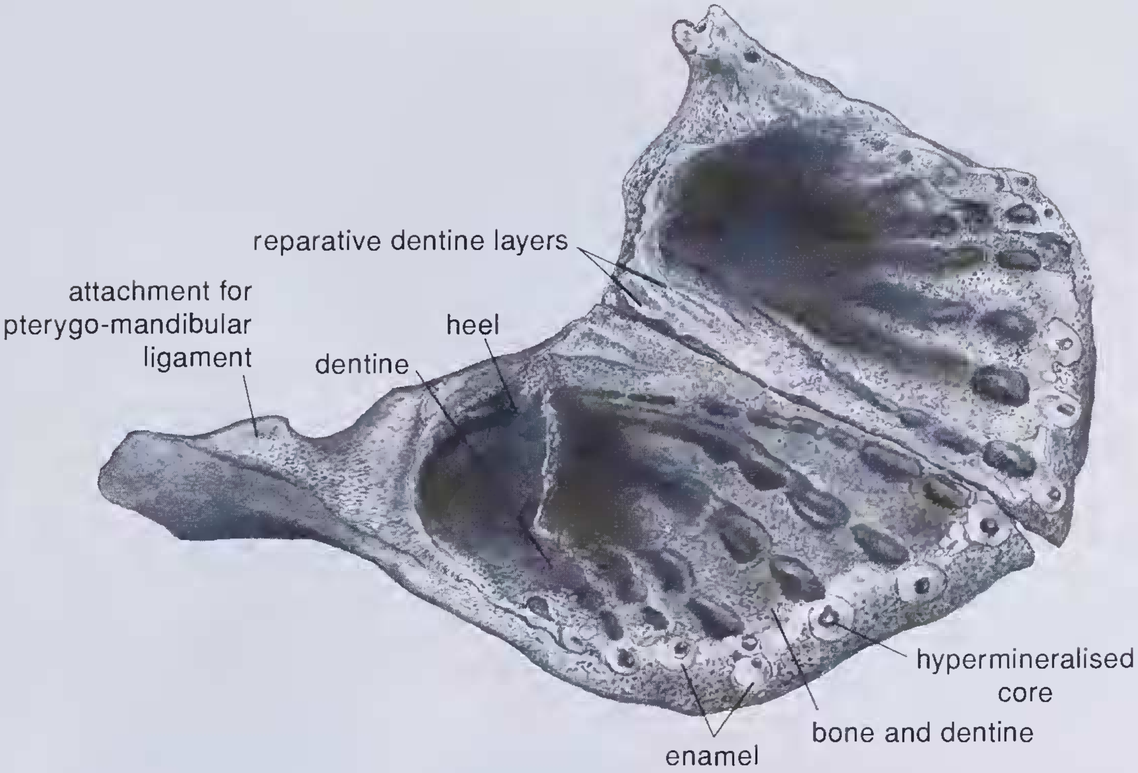

reparative dentine layers
attachment for pterygo-mandibular ligament
heel
dentine
hypermineralised core
bone and dentine
enamel

FIG. 21. *Adololopas moyasmithae* gen. et sp. nov. Oblique view of pterygoid plates of the holotype showing up the detail of bone, dentine and reparative dentine. Compare Figure 17B. Note particularly the presence of white tissue representing the enamel-covered surface around the teeth and forming a layer on top of bone between the distal teeth.

not etch as easily as the outer dentine layers.

The naming of this dentine is important. It is not interdenteonal in origin, it has poorly developed tubules, and occlusally it merges with pallial dentine, but at the opposite end it grades into bone with no distinct boundaries. The function of this dentine is to provide an outline on which the distal tooth was deposited. We consider that it should be called 'pedestal dentine' (Smith, 1985: 629). Pedestal dentine is a primary dentine joining pallial dentine to the bone of attachment.

MORE PROXIMAL TEETH. The second and third teeth from the outer edge of the plate have most characters in common with the last tooth. The second tooth overlaps the third tooth directly; most of this contact takes place between the compact dentine of the teeth, but towards the occlusal surface the pallial dentine of the two teeth are in contact (Fig. 23A,C). No sign of the pedestal dentine as described in the distal teeth can be seen in these older teeth. Presumably it was there originally, but it has been resorbed to allow other dentine to develop in its place. The initiation of this resorption is visible in the pulp cavity (Fig. 23A,C). The compact dentines of the second and third teeth are contiguous, and in some places the only way of distinguishing them is the fact that the canals diverge slightly at the junction. The pulp canals tend to be long and relatively straight, but they are interconnected irregularly (Fig. 24C-E).

The fourth and more proximal teeth become less prominent as a result of wear (Figs 17B, 21). They are composed of continuous core (compact) dentine, but with a relict of pallial dentine in some places.

Against the basal pulp cavity, it is possible to distinguish the base of the dentine columns in the core of the teeth (Fig. 24E-G). These ends are rounded in vertical section, an indication that there was continuous deposition around them by a layer of cells. The dentine formed in these positions has the same internal structure and colouring as the dentine higher up in the tooth; the only real difference is that the dentine has less obvious tubules away from the basal pulp cavity.

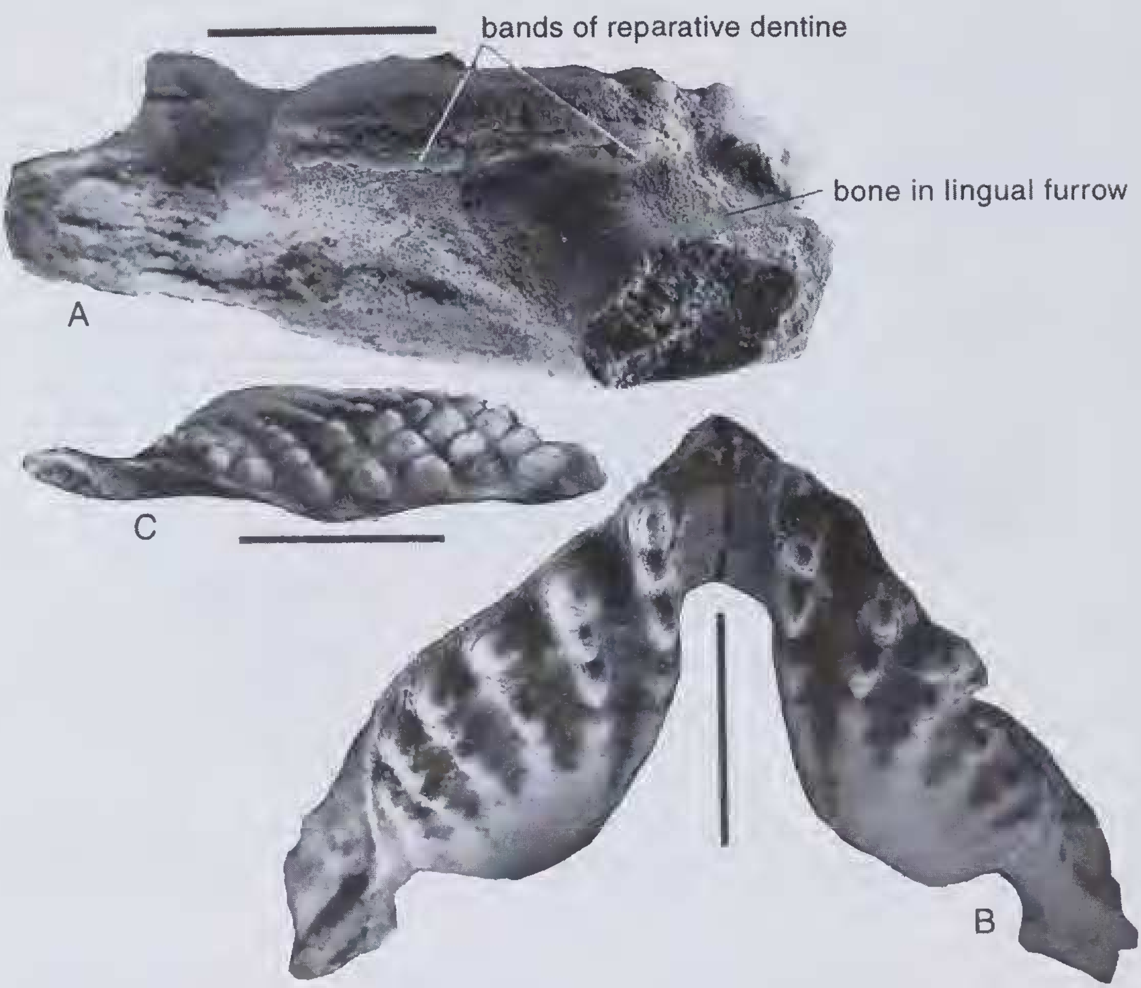


FIG. 22. *Adololopas moyasmithae* gen. et sp. nov. A, lingual view of the mandible of the holotype, with the right side of mandible removed; note the bone in the lingual furrow and the bands of reparative dentine along the basal edge of the dentine of the plate, with solid dentine dorsal to it. B, dorsal view of same with the two parts together; the specimen is tilted with the anterior upwards to show the anterior teeth against the bone. C, lateral view of WAM931.1.221 to show the curvature of the plate. Scales = 10mm.

Dentine tubules are abundant close to the basal pulp cavity (Fig. 24E-G). Although the pulp canals thin out towards the occlusal surface, we have been unable to distinguish any clear evidence of intratubular or peritubular dentine (Baume, 1980). There could be two possible causes — the thickness of the sections studied which cover up the boundaries of such layers, or to the fact that no such deposits are present, and the the pulp canals become wider towards the basal pulp cavity.

We have not had sufficient material to cut horizontal sections of a tooth to observe the pattern of extinction under crossed polars such as occur in petrodentine. SEMs also show the fibre bundles in this dentine clearly, as on the right and left sides of Fig. 27B. The following features are also inconsistent with the dentine being petrodentine (Smith, 1984); dentine tubules are present widely through the tissue — these are visible in both thin sections and in SEMs; the whole dentine is stained brown, whereas petrodentine is clear; and, the dentine is made up of tissue laid down at the base of each column (Fig. 23E-G), and is devoid of tissue that could be interpreted as having been laid down from a special layer of petroblasts.

An isolated tooth-plate of WAM931.1.221 (Fig. 18), from which the dentine has been separated from the pterygoid bone, has been cut in an oblique transverse section about two teeth in from the margin. The section has been subjected to SEM examination (Figs 27-29), and the adjacent

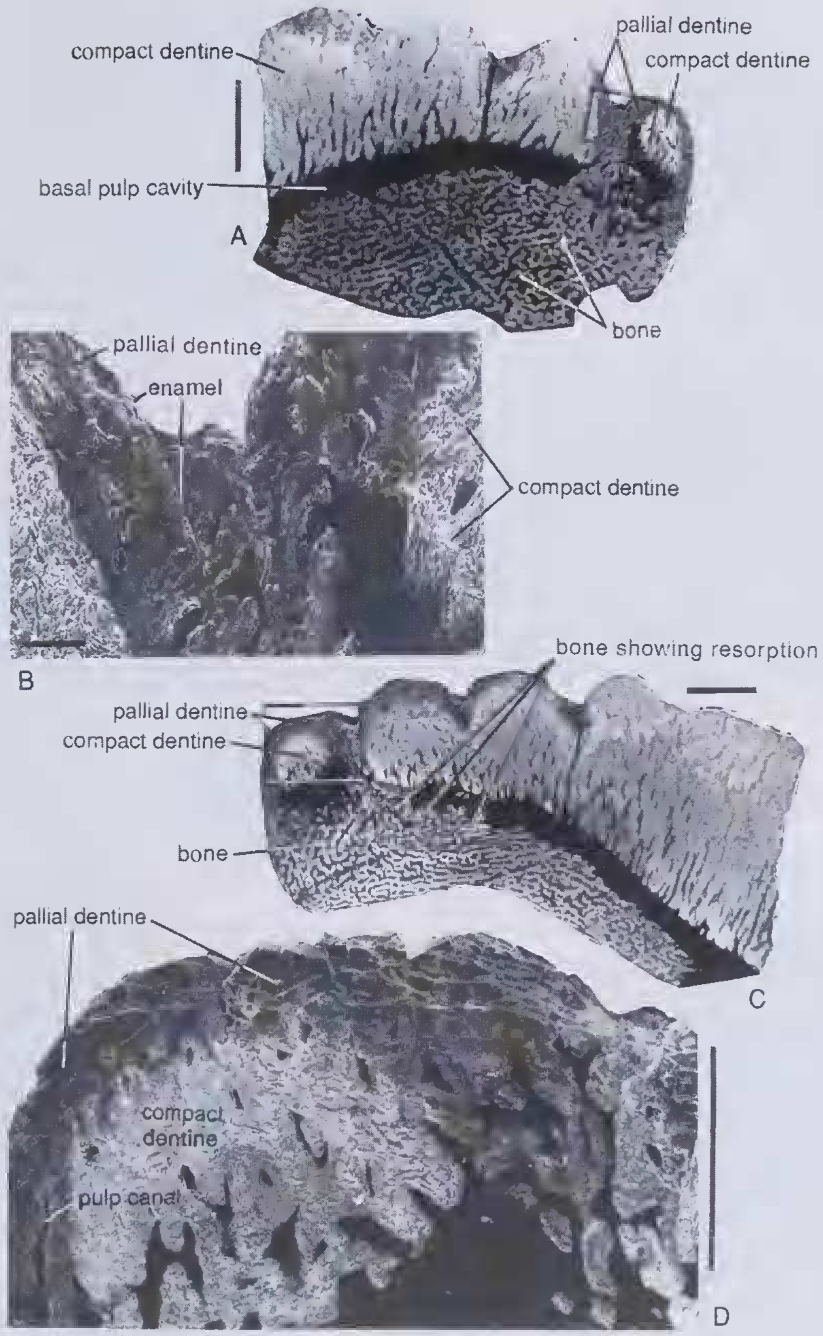


FIG. 23. *Adololopas moyasmithae* gen. et sp. nov. A, C, SEMs of two sections cut from a tooth row from WAM931.1.221; note the early initiation of compact dentine in the last formed tooth surrounded by a mass of dentine supported at its base by bone and dentine which extend up from the basal pulp cavity. This outer layer is lost on much of the second teeth. Note also the large open space of the basal pulp cavity below the tooth row, and the structure of the supporting bone. B, enlargement of the junction of the last two teeth on A, as outlined on A. The enamel which extends down into the tissue is labelled; the junction between the two layers of compact dentine and the surrounding tissue is obvious. D, enlargement of the distal tooth of C; on the right side note how the pedestal dentine extends up around the compact dentine. Scales A, C = 1mm; B = 0.1mm. D = 0.5mm.

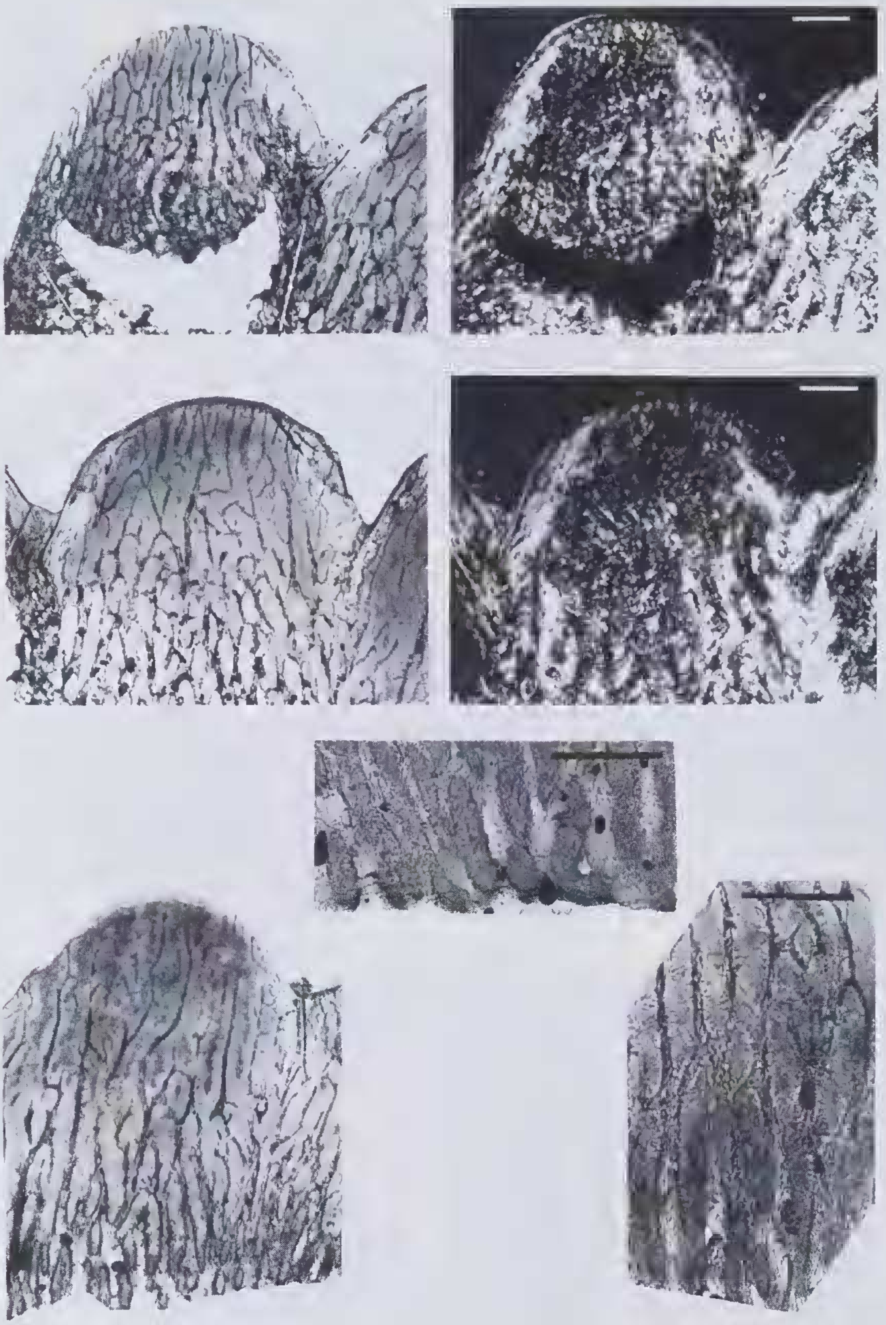


FIG. 24. *Adololopas moyasmithae* gen. et sp. nov. A, B, optical thin sections of the most distal tooth shown in an adjacent section in Fig. 23B; A is in plane polarised light and B in crossed polarised light. This shows the bone and the pedestal dentine extending up into the base of the tooth. C, D, the second tooth along the tooth row; C is in plane polarised light and D in crossed polarised light. Note the absence of pedestal dentine built into the tooth on the right side. E, an even more proximal tooth showing the basal pulp cavity at the base, and the long regular pulp canals which divide more extensively at the base than at the top of the tooth. F, G, two sections from the base of teeth to show the pulp canals running from the basal pulp canal, and also a number of dentine tubules extending into the tissue. Scales A-E = 0.25mm; F-G = 0.3mm.

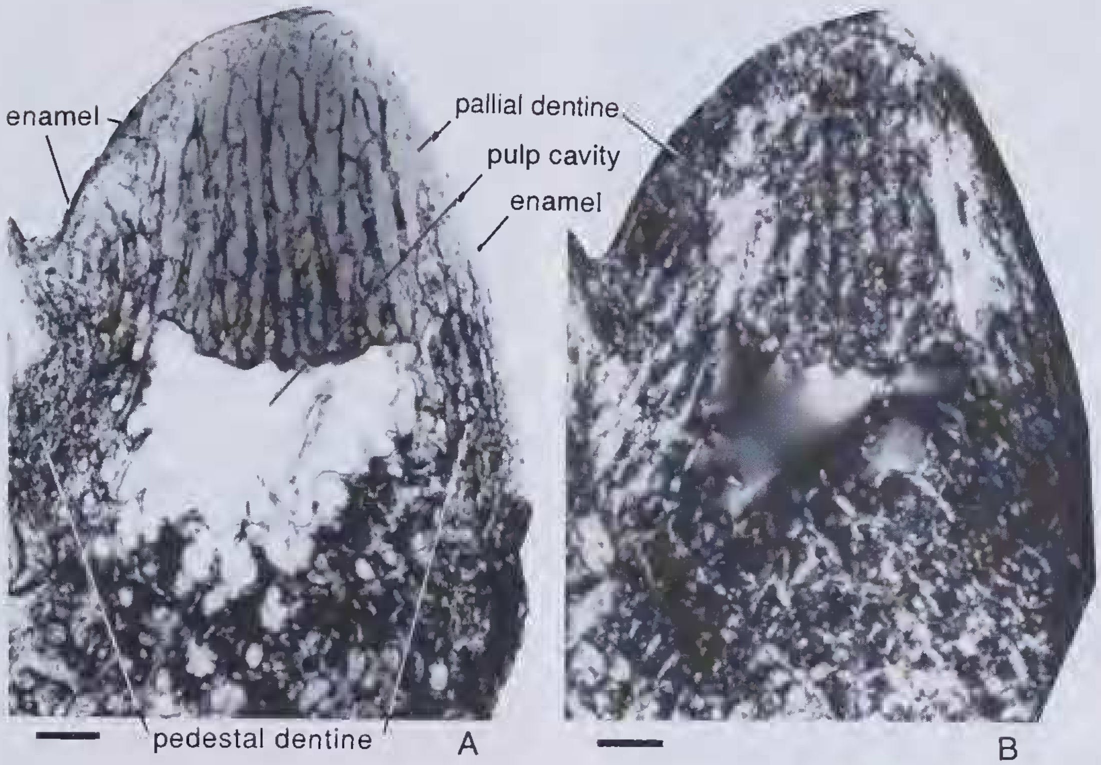
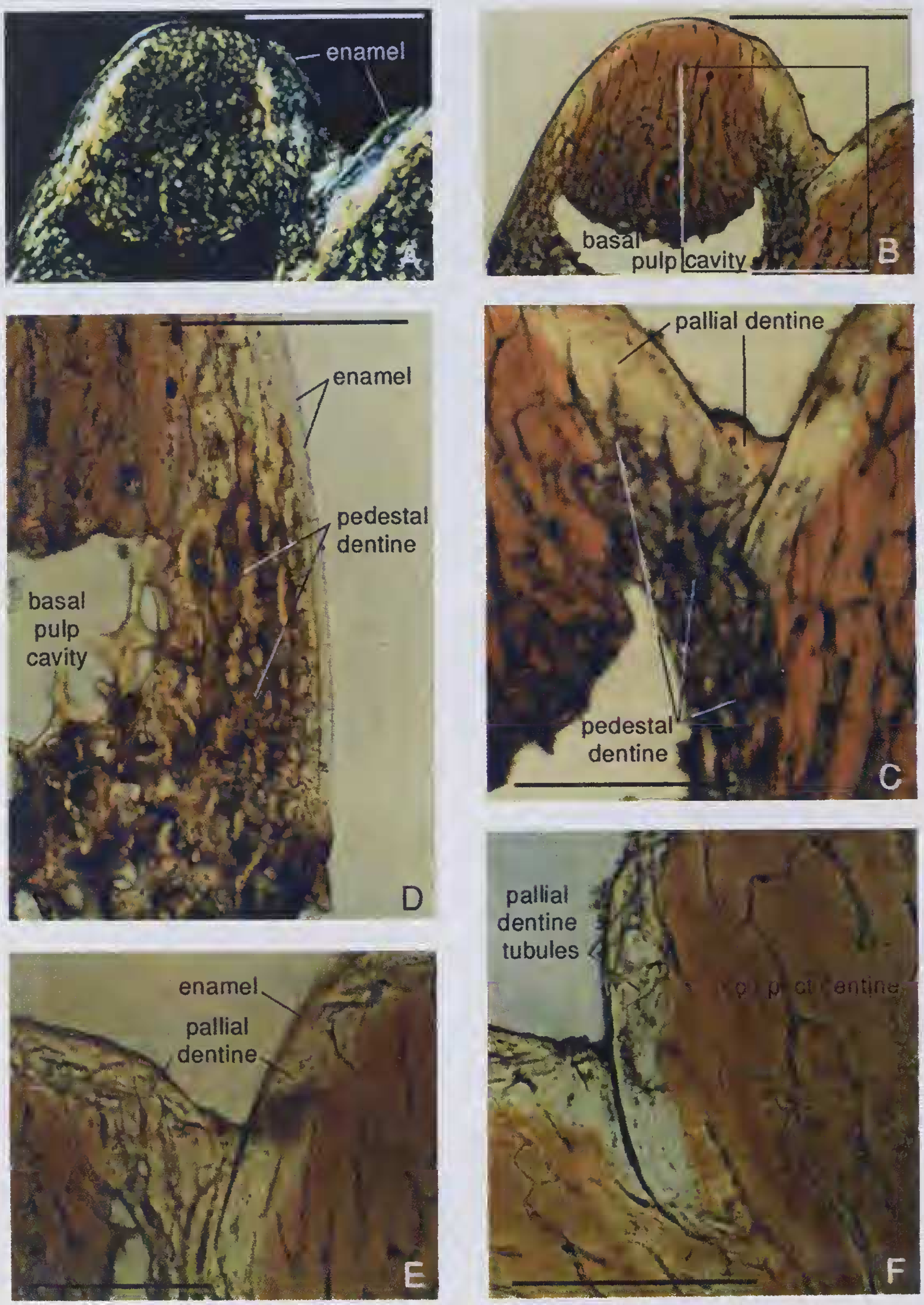


FIG. 25. *Adololopas moyasmithae* gen. et sp. nov. Optical photograph of the distal tooth of a second cut through WAM931.1.221. A, under single polarised light; B, under crossed polarised light. This specimen shows in better detail the bone and pedestal dentine as in Fig. 23. Scales = 0.25mm.

parallel section has been cut for work on the optical microscope. These sections show much detail of the tissue in the valleys between the tooth rows and its relationship to the basal pulp cavity. As indicated above, the valleys between the tooth rows are filled with what appears to be coarse dentine in natural light. Across this whole section (Figs 27A, 28A, 29), some of this inter-tooth-row dentine lies at the occlusal surface of the plate. The contact with the adjacent tissue of a tooth (compact dentine) is sharp, and there is no evidence of intergrowth of the intervening pallial dentine by pulp canals turned laterally from the pedestal dentine. The dentine in these valleys is formed of bands of tissue around pulp canals (Figs 27B,C, 28A, 29), and these bands are made of tissue like the compact dentine cores of the teeth. Many of the pulp canals are turned parallel with the occlusal surface, but deeper in the tissue the canals join and form a more continuous layer. The boundary between the filling tissue and the underlying core tissue is shown in Figs 28A, 29.

The space between the last and second last tooth on the right in Fig. 27A is shown in detail in Fig. 27B-C. It shows the fine structure more clearly than elsewhere on the section because it is the most recently formed unit between the tooth rows, and it lies over a patch where the tooth-plate surface is supported to the pterygoid bone as described above. This SEM shows no fine structure between the masses of dentine in the inter-tooth-rows, but some fine tissue must have been present in the original. Such material appears on the untreated specimen as whitish substance lying between the darker dentine columns (Fig. 17B). Thin sections of this material (Fig. 30) show that it is composed of bone which does not show up well on SEMs. Figure 27B,C are also important because at the base of the column the remnants of pterygoid bone supporting the dentine, are seen. This bone represents the hard columns of bone which appear in Figs 18-19 between the open spaces below the radial tooth rows. Fig. 27 B,C shows a slight enlargement in which the dentine in the canals meet the bone, and shows the way in which the bone is surrounded by dentine growing over its surface away from the pulp cavity. In part, this provides an understanding of why the canals in the inter-tooth rows are oblique to the rows in the teeth, and it also shows the similarity in struc-


enamel
A
basal
pulp cavity
B
enamel
pedestal
dentine
basal
pulp
cavity
D
pallial dentine
pedestal
dentine
C
enamel
pallial
dentine
E
pallial
dentine
tubules
compact dentine
F

ture between the dentine in the tooth cores and the inter-tooth-row spaces. It also demonstrates why the boundary between the inter-tooth dentine makes a sharp boundary with the tooth dentine.

Figure 28A shows the third tooth from the right in Fig. 27A, together with the tissue occupying the inter-tooth-row spaces. Because of the obliquity of the section in Fig. 27A, Fig. 28A is an older tooth than the one shown on the right side of Fig. 27A. Note the hard white compact dentine in the core of the tooth and the darkish layer on each side. An enlargement of the inter-tooth-row (Fig. 29) shows the sharp contact between the tooth dentine and the darker tissue between the tooth rows. The dentine in the inter-tooth valleys consists of largely globular masses separated by light coloured substances, as mentioned above. As can be seen from the growing edge of a plate, bone occupies the spaces between the tooth rows (Figs 17B, 21). With increasing age, dentine is deposited from pulp canals which grow up into the bone, with bone lying between dentine. Finally, the heel of the dentine plate is formed by the exclusion of bone, so that the heel is made entirely of compact dentine.

Figure 30 shows stages of the development of this dentine. Bone, with the osteocyte spaces clearly preserved, is shown surrounded by dentine and its pulp canals. The newly formed dentine beginning to occupy the spaces between the bone is shown on Fig 27B, C. The dentine which forms in the valleys between the tooth rows is of the same type as the hypermineralised dentine (compact dentine) that forms the cores of the teeth.

This new genus shows an intermediate stage in the development of a continuous pulp cavity beneath the dentine, as is shown in Mesozoic and later species. The dental plate in *Adololopas* is still firmly attached to the pterygoid or the prearticular at numerous points (Figs 18, 19, 20). It still retains some bone and intergrowing dentine in the valleys between the tooth rows. Evolution in later lungfish reduced the bone, and the dentine of adjacent tooth rows joined up laterally to make a continuous layer of dentine across the plate. Of course, associated with this change are the changes in dentine structure which have been described by many authors such as Denison (1974) and Smith (1984).

REMARKS. The arrangement of the bones making up the posterior part of the skull roof is problematical, but enough is known to make the distinctiveness of the roof apparent. The posterolateral edge of I carries an articulating groove indicating either that Z fitted around the corner of that bone, or a loose Y_2 was present. The shape of the operculum with its inturned dorsal edge is of great value in determining the presence of bones on the posterior part of the skull. Although Y_2 and Z were not preserved, it is possible to show that they were present originally because the operculum fits neatly against the bone 8 and turns inwards against the Y_2 and Z. On this reconstruction it becomes apparent that the genus was completely different from *Jarvikia* and *Gnathorhiza.*

A further complication is that the canal running forwards from I apparently enters a large bone which is situated too far posteriorly to be an X, and can only be a modified Y_1. Judging from the embayments in the flanks of J, and from the position of the canal exiting anterolaterally from J into what normally is K, X must have had a relatively small contact with J, but the shape of its contact with 3 shows that it expanded laterally; K had a large contact with J (Fig. 1), and its anterior outline remains unknown. The position of K relative to X and L is a matter of importance. In *Dipterus valenciennesi*, K is a small bone between X and L; but with the increased size of K and the anterior position of X in *Adololopas*, L is further forward also. Unfortunately we do not have an X or a K to check if a lateral line canal joins the two bones.

Too few specimens are known to permit a discussion of the variability of the species except for one point- the ornament on the pectoral girdle. On WAM931.1.221 the anterior edge carries closely spaced pustules, but these are not present on ANU49213. Other features of both cleithrum and clavicle are closely comparable.

Comparison should be made with the tooth plates of *Scaumenacia curta* Whiteaves, the best

FIG. 26. *Adololopas moyasmithae* gen. et sp. nov. A, B, distal tooth as illustrated in Fig. 24A, B, emphasising details of dentine structure; A, is in crossed polarised light. C, an enlargement of B to show details of the tissue containing pulp canals but lying outside the enamel of both the teeth. Note also the resorption of the second last tooth, now occupied by pedestal dentine of the distal tooth. D, enlargement of the edge of the distal tooth shown in Fig. 25A; note the thick enamel layer, the pedestal dentine and the bone beneath it. E, contact between the distal tooth and the preceeding one, showing pallial dentine in both, but with the dentine tubules difficult to observe. F, contact between the second and third last teeth, showing the dentine tubules in the pallial dentine and the abundant tubules in the adjacent compact dentine. Scales A, B = 1mm; B = 0.25mm; D-F = 0.5mm.

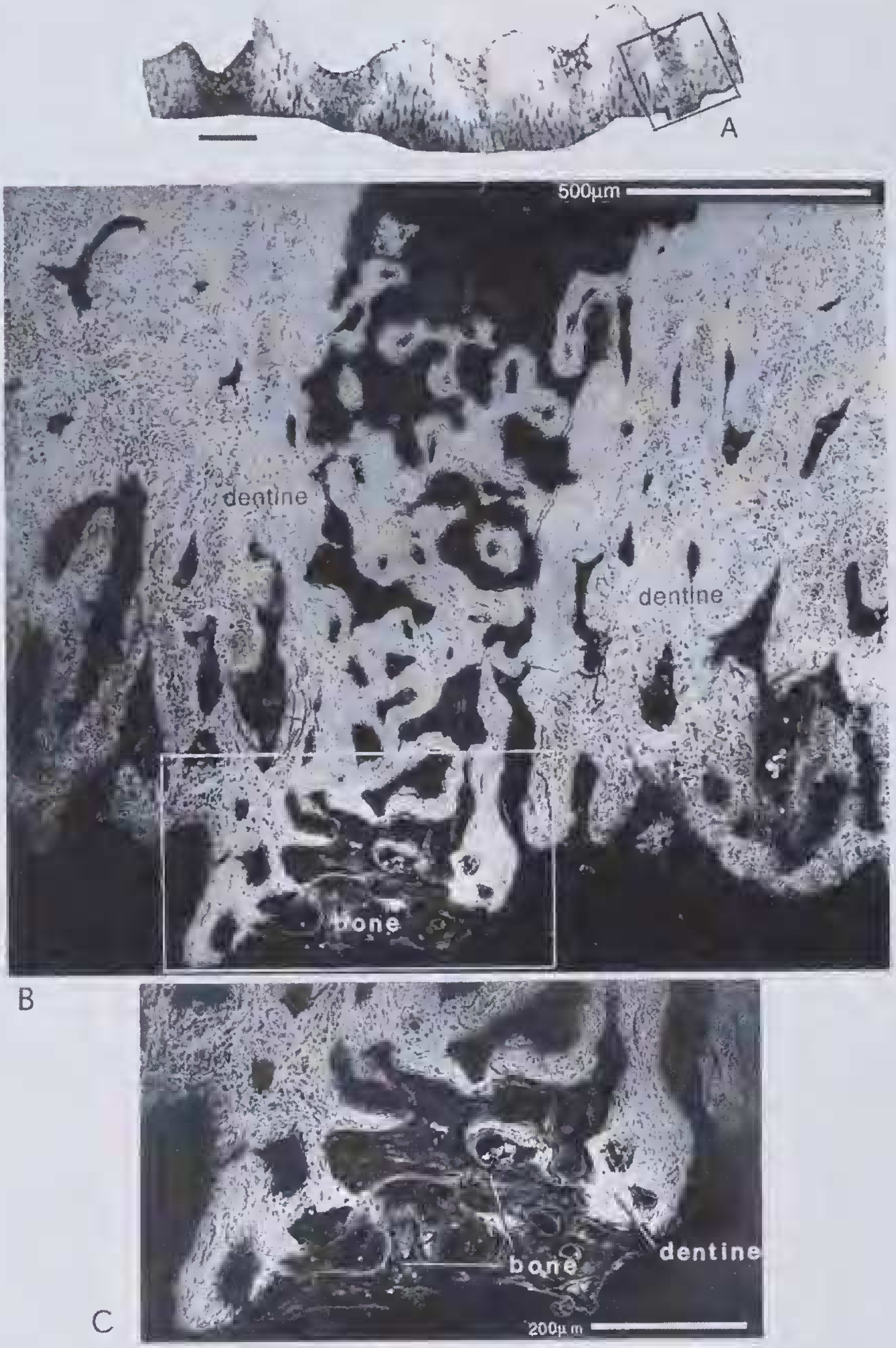


FIG. 27. *Adololopas moyasmithae* gen. et sp. nov. A, SEM of transverse section across the anterior part of WAM931.1.221 showing the teeth and the dentine filling the inter-tooth-row spaces. B, section through the last inter-tooth-row space outlined on the right of A showing the texture of the dentine in the teeth and the orientation of the pulp canals. A small amount of bone lies at the base of the dentine. C, an enlargement of the space outlined on the basal part of B showing the dentine-bone contact, and the formation of the new dentine around the bone spaces. Scale A = 10mm.

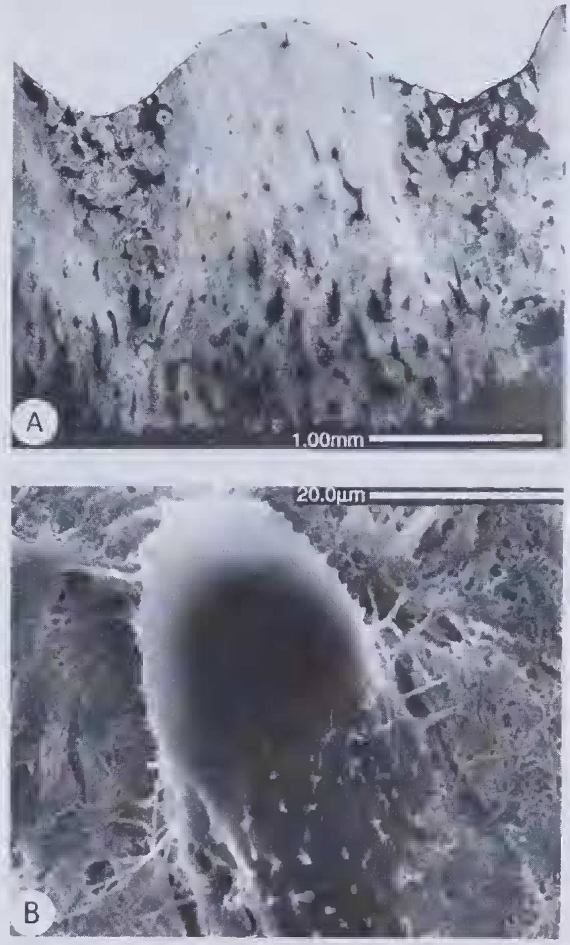


FIG. 28. *Adololopas moyasmithae* gen. et sp. nov. A, third tooth from the right in Fig. 27A and the infillings of the inter-tooth-row valleys. B, dentine close to the base of a pulp canal adjacent to the basal pulp cavity; note the branching nature of the dentine tubules.

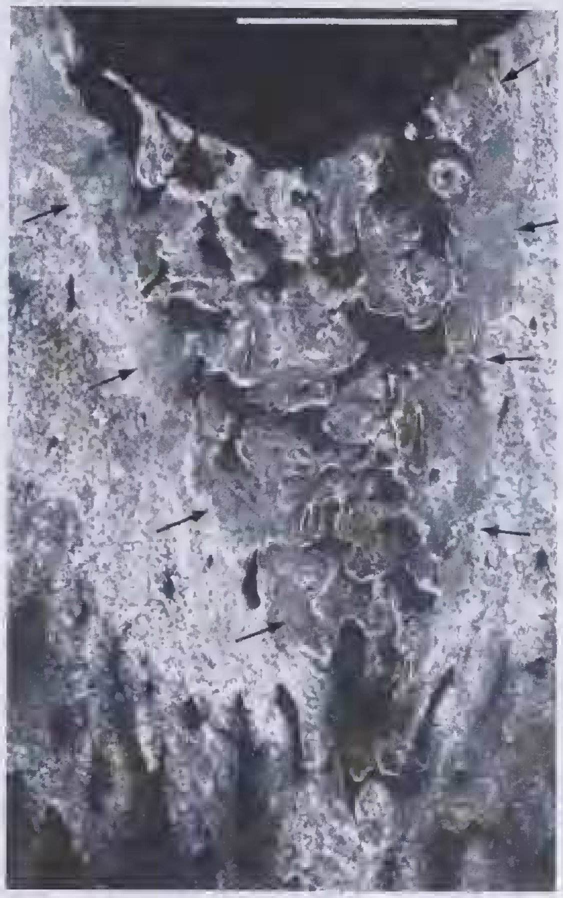


FIG. 29. *Adololopas moyasmithae* gen. et sp. nov. Enlargement of the space to the left of the third tooth from the right in Fig. 27A showing the contact (arrowed) between the compact dentine of the tooth core and that of the space between the teeth. Note the black gaps between the dentine that seem to have no tissue in them. They are filled with thin bone which does not show up on SEMs, but is well shown in optical thin sections (Fig. 30). Scale = 0.5mm.

known of the Frasnian genera from elsewhere in the world. These have been described by Denison (1974), Smith et al. (1987), and Cloutier (1996). Denison thought that the plates of *S. curta* had grown in the same way as those of *D. valenciennesi*, but their histology was entirely different. Unlike *D. valenciennesi*, the specimen of *S. curta* sectioned by Denison (refigured here as Fig. 32E, F) had well-differentiated dentine and bone, separated by small resorption pulp cavities at the base of at least the most labial tooth; and the dentine canals, though branched, were much more regular than those of *D. valenciennesi*. Denison claimed to have observed a small patch of pleromic dentine in the most proximal of the teeth in the section figured, but not in any of the others. We have examined the specimen and have been able to confirm most of the points of Denison's description, although the mounting medium has crystallised, destroying the clarity of much of the slide. We have found a small patch of what Denison refers to as pleromic dentine, but we do not consider that it has any importance. Smith et al. (1987) have given a more complete account of *S. curta*, and have added more histological information.

Cloutier (1996) has figured palatal plates of *S. curta* which show clearly the suture between the two plates, the elongated lingual row on each plate, and the extension of the tooth rows to the heel of the tooth. In addition, his specimen is recorded as having 'small tubercles of enamel infrequently added posteriorly and posterome-

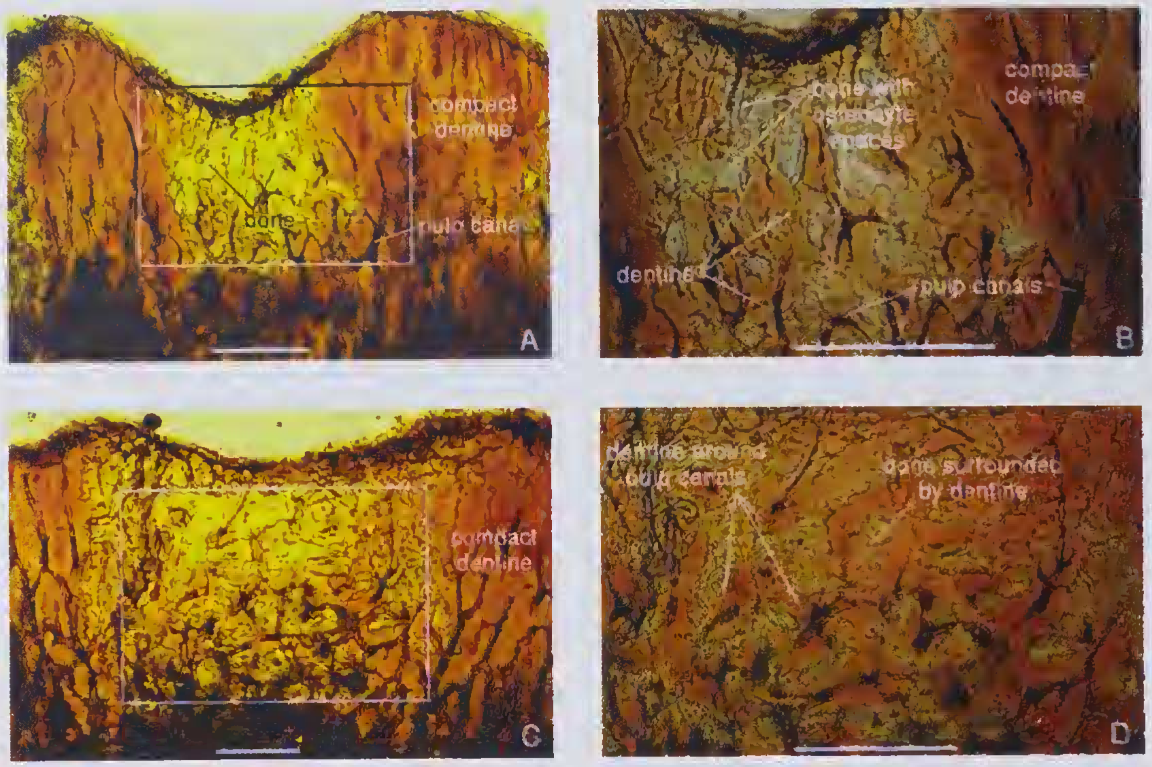


FIG. 30. *Adololopas moyasmithae* gen. et sp. nov. Optical sections cut parallel with the section in Fig. 27A. A, B, a section in which the amount of dentine is only partly developed; C, D, a section in which the bone is more extensive. B and D are enlarged areas of A and C respectively. In A and C the pulp canals are surrounded by compact dentine, the dentine of adjacent canals being in contact. In D the pulp canals are not so common, and places where bone is surrounded by dentine to form a core, are well shown. Osteocyte spaces are present in the bone. Scale = 1mm.

dially to repair the heel of the tooth plate', and he comments that there is a thin layer of enamel covering most of the surface of the tooth plate. The first point indicates that the primitive pattern of denticles is maintained in this genus. The second point is difficult to accept because enamel is laid down as a tissue on the outer surface of a tooth, and should not be present in the intervening furrows between the tooth rows, unless the adjacent tooth rows converge. Such does not seem to be the case. We also note that Cloutier's fig. 6, seems to show a broad band of exposed bone mesial to the lingual row of teeth, but Smith et al. (1987, p. 315) comment that there are simple sheets of dentine in that region. In addition, they note that there is no bounding layer of enamel around the outer margins of the teeth. It seems that in these respects *S. curta* is closer to *Adololopas* than to later genera.

We have been able to cut thin sections of two small topotypic tooth-plates of *Scaumenacia curta* given to KSWC by Denison. Both oblique transverse and vertical sections are available, one of the vertical sections being of the most labial tooth in a row. All sections show the usual enamel layer over a layer of pallial dentine. Low down on the tooth, ventral to the pallial dentine, is a coarse open tissue, as in *Adololopas*. This tissue is continued downwards into the bone, and its detail is like that of the bone, (though without osteocyte spaces). We therefore refer to it as pedestal dentine as in *Adololopas*. It is heavily stained with iron compounds, and the internal structure in some places is difficult to determine. On the other hand, it is possible to recognise dentine canals extending into it from the more medial part of the tooth (Fig. 32A, B). The core of the tooth is composed of hypermineralised dentine (referred to by Denison (1974) as trabecular dentine, and by Smith et al.,1987, as petrodentine) that has minimal iron-staining, and shows pulp canals like those figured by Denison (1974, fig. 5), i.e., they are essentially vertical but divide and rejoin to form a coarse reticulum. It is possible to recognise a few small dentine tubules extending from the dentine canals into this tissue, but the tubules are

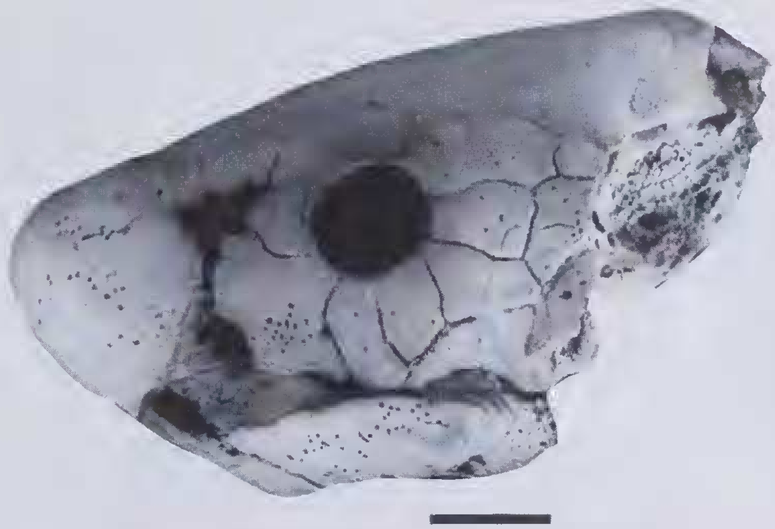


FIG. 31. Lateral view of a head of *Chirodipterus australis* Miles. Note the shape of the lip outline which has been dotted in where bone is missing. Scale = 10mm.

irregular in their distribution and they are much shorter and narrower than those in ordinary dentine. In cross-polarised light, the cross pattern reported by Smith in petrodentine has been observed.

In a section along a tooth row (Fig. 32E,F) the column of petrodentine extends almost up to the crest of the tooth, demonstrating that its deposition began shortly after the trabecular dentine was formed in that region. In teeth that have completed growing, the petrodentine lies directly on the basal bone. In more recently formed teeth there is a basal pulp cavity which is small and gives a space into which the petrodentine grows. This basal pulp cavity is small in the most recently added tooth in Denison's specimen (Denison 1974, fig. 5A,B). In the ANU specimen it is large and has a clear opening into which growth may occur. In more proximal teeth, no basal pulp cavity is present. Presumably it has been filled by downwardly growing petrodentine. This is unlike the situation in *Adololopas*, in which the basal pulp cavities remain open under a number of teeth and into the more solid proximal parts of the plates.

DISCUSSION OF LONG HEADEDNESS IN DIPNOANS

Schultze (1992) pointed out that some Devonian dipnoans are long-headed because of the length of the snouts and others because of the length of the posterior parts of the heads. This analysis makes many useful points, but it has some difficulties which we will discuss here because *Adololopas* has a long cheek and should fall into the second of Schultze's categories. In our view the length of the head is related to a number of functional factors including gathering food, reduction of food, and the position of the gill chambers.

The first problem to us is one of misinterpretation of data; e.g., the reconstruction of the snout of *Uranolophus wyomingensis* (Schultze, 1992, fig. 5C). In our view, he shows the eye placed too far forward. This position is not explained in his text, but quite clearly the elongate bone lateral to L_1 on Schultze's fig. 5C should be a bone 3, and the eye should be placed ventral to it. His value of l^d for this species is incorrect. What is more, the posterior part of the head is more elongated than it should be in relation to the snout with which it is figured, a point that is illustrated by a comparison of the figures of Denison (1968, fig. 3A) and Campbell & Barwick (1988b, fig. 2C). With the eye put into its correct position, this genus shows a greater comparison in skull outline to the adjacent figure of *Soederberghia groenlandica* in Schultze's paper.

Schultze's (1992) discussion of *Holodipterus* is also erroneous in a number of respects. Details of the morphology of that genus are set out in Pridmore et al. (1994). For example, the palate has a denticulated surface with denticles on the parasphenoid (Pridmore et al., 1994, figs 8, 47, 49). The denticles are subject to renewal at several periods during the life history of an animal, and individual denticles are covered with intervening 'primitive' dentine during some phases of renewal (Schultze, 1992: 42). This pattern is totally unlike that of *Speonesydrion* (Campbell & Barwick, 1983; 1984), a comparison suggested by Schultze. The marginal ridges are present, and are more obvious on some species, especially at some stages of resorption (Pridmore et al., 1994, figs 4, 29, 73, 96), but in other specimens they are expanded depending on how much resorption has taken place. Contrary to the statement by Schultze (1992: 42), the preorbital cheek has the same cutaway ventral edge as in *Griphognathus*, as was well shown by Campbell & Smith (1987, fig. 8). Schultze (1992) suggested that it is like the sur-

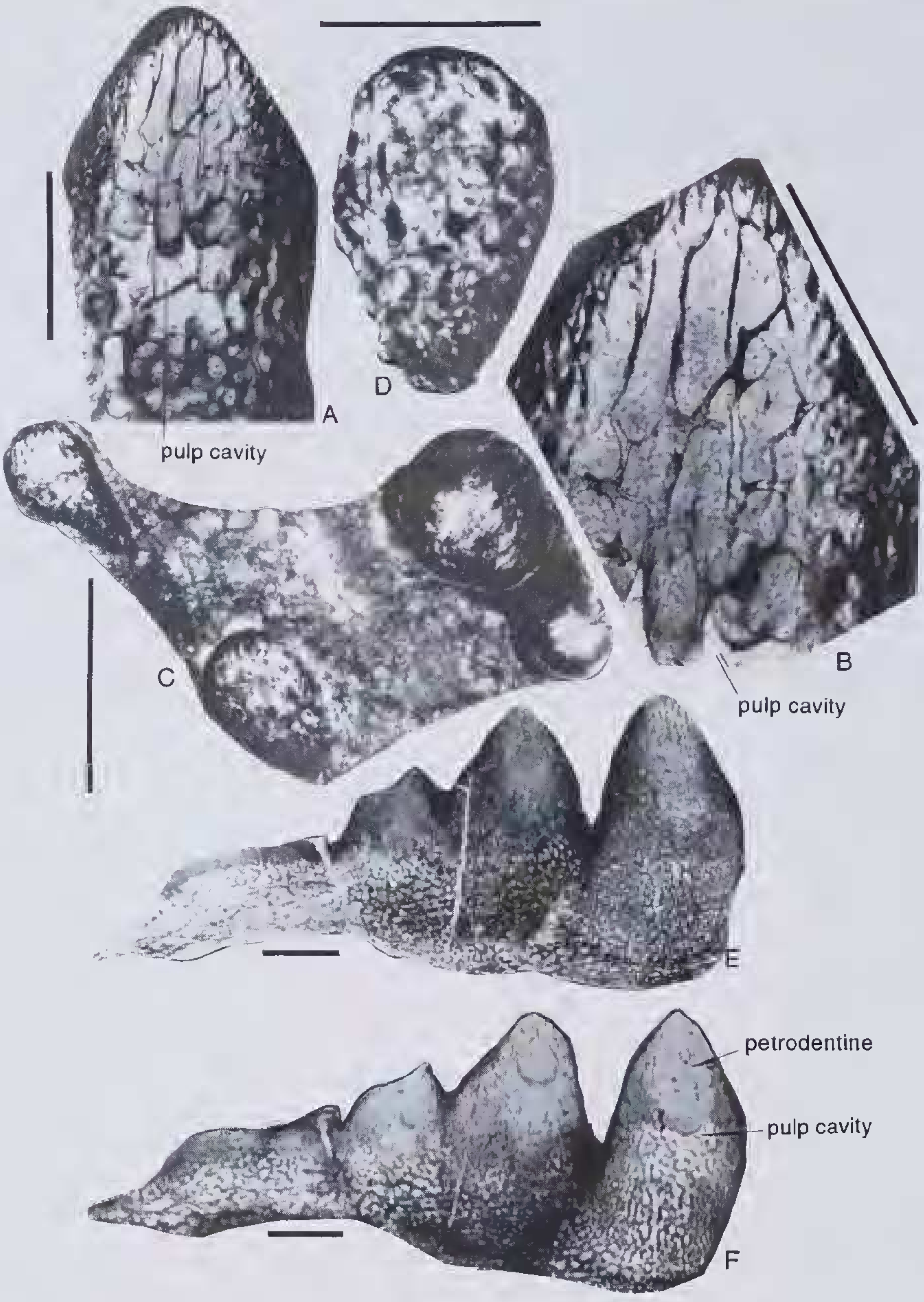


FIG. 32. *Scaumenacia curta* Whiteaves. A-D, optical sections of ANU49092. A, vertical section of the most distal tooth showing the large basal pulp cavity surmounted by dentine, surrounded by dark tissue into which the pulp canals extend. B, enlargement of same, showing the absence of dentine tubules and the cross-textured mass of dentine. C, part section of tooth rows cut from the same specimen; note that close to the tip of the tooth the hard central dentine is present. D, enlargement of the bottom left tooth in C; note the pulp centres within the dentine. E, F, two views of the section figured by Denison (1974, fig. 5) . The mounting medium has been recrystallised making the definition worse than in the original figures. E is under single polarised light, and F is crossed polarised light. Note the absence of basal pulp cavity beneath any tooth. Scales A-C = 1mm; D = 0.5mm; E, F = 1mm.

face of *Chirodipterus*, but in fact there are no similarities; it is difficult to see how such a conclusion could be made. In comparing Fig. 33 in this paper with fig. 8 in Campbell & Smith (1987), we note that the ventral edge of the cheek in *Holodipterus* has a considerable gap between the edge of the cheek and the mandible. In addition, the marginal ridges on the palate are nothing like the ridges of *Chirodipterus* or *Speonesydrion* (Campbell & Smith, 1987; Campbell & Barwick, 1984) as suggested by Schultze (1992). Nowhere does Schultze's work comment on the method of making marginal palatal ridges by resorption of the surface on the inner parts of the plate, or of the production of bosses on the palate by failure to resorb parts of denticulated surface during successive episodes. Although when Schultze wrote there was no evidence of basihyal-basibranchial bones in *Holodipterus*, but these are now available Pridmore et al. (1994, figs 29, 32, 57).

In view of Schultze's discussion, we must emphasise that the presence of denticles in the mouth does not indicate a primitive dentition. Denticles are present in a variety of different genera, and we are in no doubt that they have evolved several times to meet different requirements. We chose to use the term 'denticulated' to characterise one group of dipnoans, because that seemed to be an obvious feature of one group. This may have been an unfortunate choice of a term, but it does not permit a misinterpretation of the remainder of the discussion.

Schultze also noted that *Holodipterus* was a food crusher in its feeding, whereas the denticulated group is not so. We point out that *H.(H.) longi* (Pridmore et al., 1994) has a mandible like that of *Griphognathus*, its median area being reduced in length. This mandible also has an adductor pit that is similar to that in other species of *Holodipterus*, and its teeth have been almost completely removed by resorption. In other words this species is different from the basic outline of *H. gogoensis*. The question we now have to ask ourselves is: does the presence of the teeth mean that the group is a tooth-plated form; or does the fact that no true tooth-plates are developed in *Holodipterus*, mean that the teeth were developed secondarily in a genus that was initially a 'denticulated' form? In connection with this argument we point out that in *Holodipterus* the teeth are different in histology from the teeth of other tooth-plated species (Campbell & Smith, 1987), and that they are resorbed periodically from the mesial part of the mouth, the evacuated surfaces becoming occupied with denticles. The latter view will be rejected by cladists because it is less parsimonious than the former since it requires two developments of teeth within the dipnoans. However, such a parsimonious view is irrelevant, in that it obscures relationships based on biological similarities. We acknowledge that such a 'parsimonious' view will be adopted by some workers, but point out that parsimony applied in such circumstances is unacceptable. In this type of enquiry, parsimony may be used to choose between two hypotheses which have equal merit in explaining a set of observations. It should not be used to generate the hypotheses. In addition, we draw attention to the quote in the paper by Schultze & Marshall (1993): 'And if you get only one tree, but you cannot explain it biologically – start all over again'.

Uranolophus is said by some workers to be different from other denticulated genera in the form of the parasphenoid. Denison in his original paper indicated that it was long and thin, stretching forwards almost to the anterior end of the pterygoids. Campbell & Barwick (1988b) attempted to show that the plate was short, rather like the parasphenoids in such other groups as *Griphognathus*, and that the boundaries of the parasphenoid outlined by Denison were cracks in the palate. Schultze (1992) indicated that the interpretation of Denison was correct, reproducing a drawing in his fig. 1 and photographs in fig. 3 to support this view. Even so, he notes that 'such a parasphenoid is unique within the dipnoans'. We wish once again to dispute his interpretation of the outline on 6 arguments. 1) So far as we are aware, the parasphenoid is a bilaterally symmetrical median bone. Even in those genera in which the dorsal edge of the parasphenoid is expanded, the shape of both dorsal and ventral edges should be symmetrical relative to the midline. This is not so in the inferred outline of Denison. 2) If the shape is as shown by Schultze, 1992, fig. 1B, with the posterior outline skewed, this does not match the position of the dorsal edge as shown by Campbell & Barwick (1988b, fig. 1E). 3) The pituitary is known to have a double origin — part of it is a ventral growth from the braincase, and the other from the pharynx. In *U. wyomingensis* the pituitary fossa (Campbell & Barwick, 1988b, fig. 1E), is situated about one third of the length of the palate from the posterior end, which is its position in other Devonian dipnoans. What is more, the palate is thin, and the hypophysial stalk would have to be situated in approximately the same position. The organisation is very similar to that of *Griphognathus whitei*, in which the parasphenoid is of normal Devonian type. 4) We simply controvert the view that other specimens of *U. wyomingensis* in which the palates are incomplete show that the details indicate an elongate parasphenoid. 5) The palate is not thick, but it has thickened edges in certain places as is common in *Griphognathus*. Such thickenings are correlated with its peculiar mode of feeding (Campbell & Barwick, 1988b, fig. 7A). This is the specimen on which Schultze (1992, fig. 1B) is based, and in which the anterior end of the parasphenoid follows the outline of the depression. 6. Comparison with outgroup species such as *Diabolepis* does nothing to add to the argument. What such argument shows is that attention to comparative studies with genera of doubtful affinity causes observers to view what they think are appropriate structures, rather than what is to be seen. It biases basic morphological work towards bad observation. In summary we see no reason apart from cracks on the palate to assume that the parasphenoid is long and narrow as suggested by Denison (1968) and Schultze (1992).

We were mistaken in stating that the 'denticulated' group had no adsymphysial plate in the lower jaw of *Griphognathus* (Campbell & Barwick, 1984, p. 163). Such a plate is not clear in *G. whitei*, but it is present in *Griphognathus sculpta*. This item will have to be removed from the features used to outline the 'denticulated' group (Campbell & Barwick, 1990).

The group of *Griphognathus*, *Rhynchodipterus*, *Soederberghia* and *Fleurantia* is not monophyletic; Schultze (1992) recognised this. *Iowadipterus* cannot be related to *Holodipterus* as a long-headed form in which the the mandible is short. Compare the mandible of *H.(H.) longi* (Pridmore et al.,1994, fig. 33) with that of other specimens of *Holodipterus* figured elsewhere in the same paper. *Holodipterus* is a member of the so-called 'denticulated' group, which has become shorter headed than other members of that group as a result of the development of marginal teeth which are progressively resorbed. It is not possible from available material of *Iowadipterus* to indicate what its relationships are. Further evidence of the structure of its palate is necessary.

Schultze (1992) was of the opinion that the longer posterior part of the skull permitted a larger mass of adductor mandibulae musculature to fit under the skull roof; this is certainly correct for *Iowadipterus* which is also characterised by a very forward position of the eye. Comparison of Schultze's (1992) figures of *Iowadipterus* and *Holodipterus* (Fig. 3) show that the forward position of the eye relative to the median bones of the skull roof B and C, is not the only factor involved in providing a larger space for muscles, because the operculars of the two genera lie in a completely different position relative to the Y bones. In dipnoans, the anterior edge of the opercular is situated against the quadrate, which defines the front wall of the gill chamber. We conclude, therefore, that in *Iowadipterus* the gill chamber was situated further back relative to the Y bones than in *Holodipterus*. This is important because it suggests that the elongation of the posterior part of the head and the cheek is the result not only of the forward position of the eye, but also the position of the gill chamber. Consequently the functional significance of the position of the gill chamber has to be investigated as well as the space for adductor muscles. It seems probable that elongation of the head may be the result of more than one factor. In addition to muscle space and gill chamber position, we consider that elongation of the parasphenoid to roof over the buccal chamber, in which air was held prior to its being forced down into the lungs, could also be significant (Campbell & Barwick, 1988a). Information on the position and size of the parasphenoid in *Iowadipterus* is not at present available, and so we cannot make a judgement about how it fits above the gill chamber.

In summary, we see no evidence that the extension of the posterior part of the head and the elongation of the cheeks, is likely to outline a distinctive group of dipnoans.

ACKNOWLEDGEMENTS

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